A taxonomic review of Australian Greater Long-eared Bats previously known as *Nyctophilus timoriensis* (Chiroptera: Vespertilionidae) and some associated taxa

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ABSTRACT

A comparative morphological and morphometric assessment was undertaken of material from mainland Australia, Tasmania and Papua New Guinea that has previously been referred to as the Greater Long-eared Bat *Nyctophilus timoriensis* (Geoffroy, 1806). Five taxa are recognised: *N. major* Gray, 1844 from south-western Western Australia; *N. major tor* **subsp. nov.** from southern Western Australia east to the Eyre Peninsula, South Australia; *N. corbeni* **sp. nov.** from eastern mainland Australia from eastern South Australia, through Victoria to Queensland; *N. sherrini* Thomas, 1915 from Tasmania, and *N. shirleyae* **sp. nov.** from Mt Missim, Papua New Guinea. *Vespertilio timoriensis* Geoffroy is regarded as *nomen dubium* due to uncertainty surrounding provenance of the original specimen(s), the lack of a definite type specimen, and lack of sufficient detail in the original description and illustration to relate the name to a singular, currently recognised species.

This review required a consideration of two taxa not usually associated with *timoriensis*: *bifax* Thomas, 1915 from eastern Australia and New Guinea, and *daedalus* Thomas, 1915, previously treated as the western subspecies of *bifax*, occurring from western Queensland, the northern part of the Northern Territory, and northern Western Australia. *Nyctophilus daedalus* is shown to belong to a separate species group. The implications of removing *daedalus* from *bifax* are discussed in relation to *N. arnhemensis* Johnson, 1959, which is considered to be a sibling species of *N. bifax*.

The inter-specific relationships of these taxa are evaluated. A *major* species group is recognised, consisting of *major* Gray, 1844 and *N. corbeni* **sp. nov.**, while *sherrini* Thomas, 1915 is placed in a *gouldi* group. The relationships of *N. shirleyae* from Papua New Guinea remain unclear but it is provisionally placed in a *bifax* group. The relationships of *N. daedalus*, which is likely to be a composite species, remain unclear and it is provisionally placed in the *major* group. *Nyctophilus howensis* from Lord Howe Island differs from all other members of the genus and its generic status needs re-examination.

Key words: Long-eared Bat, *Nyctophilus timoriensis, Nyctophilus*, bat taxonomy, new species, Australia, Tasmania, Papua New Guinea, Timor, Microchiroptera.

Introduction

The Greater Long-eared Bat *Nyctophilus timoriensis* (Geoffroy, 1806), is considered to be the most widely distributed and largest extant member of the genus. Until recently, the prevailing concept of *N. timoriensis* was of a species extending across the southern half of the Australian continent, Tasmania, Timor and Papua New Guinea (Flannery 1995a; Bonaccorso 1998). The nomenclature and taxonomy of this species has remained confused since its description in 1806, partly because it was uncertain whether Geoffroy's material actually came from Timor, and also because the whereabouts of his specimens has remained in doubt for the past century. Timor has been regarded by many authors since Tomes (1858) as a locality error, because the genus had not subsequently been recorded from Timor. However, a single specimen of *Nyctophilus* obtained by Kitchener *et al.* (1991) from Lembata Island, Indonesia (described as *N. heran* Kitchener *et al.*, 1991), reinstated the possibility than the genus also occurs in Timor.

The mainland Australian populations of the Greater Long-eared Bat have often been referred to as *N. timoriensis timoriensis*, while larger animals from far south-western Western Australia have variously been referred to as *N. timoriensis timoriensis*, *N. timoriensis major* Gray, 1844 or *N. major*. A separate subspecies *N. timoriensis sherrini* Thomas, 1915 was recognised from Tasmania, while some authors considered that large *Nyctophilus* from Tasmania were *N. gouldi* Tomes, 1858, not *N. timoriensis* (Hall and Richards 1979; Richards 1983). The New Guinea records of the species arose from a small number of large *Nyctophilus* specimens that were tentatively assigned to *N. timoriensis timoriensis* by Hill and Pratt (1981). The prevailing nomenclature derives from Iredale and Troughton (1934) and Tate (1941). However, Iredale and Troughton regarded *major* as a synonym of *N. timoriensis*, and *gouldi* as a south-eastern Australian subspecies of *N. timoriensis*, being unaware of the presence of large *N. timoriensis* in eastern Australia. Hall and Richards (1979) recognised that *N. timoriensis* was present in eastern Australia and distinct from *N. gouldi*.

Eleven species of *Nyctophilus* were recognised prior to this study (e.g. Simmons 2005). The most widely accepted synonomy of the 22 names proposed for the genus is given in Table 1, along with the type locality and broad distribution. Six species were considered to occur on mainland Australia (Churchill 1998), four species (two endemic) on the island of New Guinea (Flannery 1995a; Bonaccorso 1998), one endemic species on New Caledonia (Flannery 1995b; Parnaby 2002), and two endemic species known from single specimens: *N. heran* from the Indonesian island of Lembata (Kitchener *et al.* 1991) and *N. howensis* McKean, 1975 from Lord Howe Island, the latter known only from a sub-fossil. Recent publications (e.g. Reardon 1999; Churchill 2008; McKenzie 2008; Turbill *et al.* 2008) recognise additional taxa within *N. timoriensis* and *N. bifax* and draw from earlier unpublished findings of this study.

Nyctophilus has been recognised for many decades as a complex genus in need of extensive taxonomic revision (Wood Jones 1925; Tate 1941, 1952; McKean and Price 1967; Hamilton-Smith 1974; Koopman 1984; Parnaby 1991; Reardon 1999). Important taxonomic studies of the genus are the revisions of Tomes (1858), Peters (1861), Thomas (1915) and the reviews of Tate (1941, 1952). Iredale and Troughton (1934) made a number of nomenclatural changes in their checklist of Australian mammals, as did Ride (1970), although each without discussing their taxonomic decisions. The most recent published taxonomic treatments are the reviews of the genus by Koopman (1982) for New Guinea species, Koopman (1984) for Australian species, and the unpublished morphological revision of Parnaby (1988).

Most species of *Nyctophilus* remain poorly diagnosed and inter-specific relationships are in considerable doubt. Past difficulties in defining species have arisen partly from an inadequate appreciation of intra-specific variation within the genus, which were impeded by the small sample sizes previously available for most taxa except *N. geoffroyi*. In particular, taxa from northern Australia and New Guinea were known from comparatively few specimens, and New Guinea species such as *N. microdon* and *N. microtis* are still poorly represented in research collections (see Bonaccorso 1998) as are the Australian taxa *N. major*, *N. sherrini* and *N. daedalus* Thomas, 1915 recognized in this study.

A further difficulty impeding resolution of species boundaries within *Nyctophilus* has been the confusing and seemingly continuous nature of morphological variation in metric and non-metric characters that have

Table 1. Synonymy of the 22 available names of *Nyctophilus*, arranged by the 11 species recognized in recent treatments (in bold), and giving their broad geographic distributions.

Synonymy	Type locality	Australian mainland	Tasmania	New Guinea	Timor	Lembata Is, Indonesia	New Caledonia	Lord Howe Is.
***Nyctophilus timoriensis* (Geoffroy, 1806)**		x	x	x	?			
Vespertilio timoriensis Geoffroy, 1806	? Timor							
Nyctophilus major Gray, 1844	Perth, WA							
Nyctophilus sherrini Thomas, 1915	Tasmania							
***Nyctophilus gouldi* Tomes, 1858**	Morton Bay, Qld	x						
***Nyctophilus geoffroyi* Leach, 1821**	Australia	x	x					
Barbastellus pacificus Gray, 1831	Unknown							
Nyctophilus australis Peters, 1861	? Western Australia							
Nyctophilus unicolor Tomes, 1858	Tasmania							
N. geoffroyi pallescens Thomas, 1913	Alexandria, NT							
Nyctophilus geayi Trouessart, 1915	Nicholson River, Vic.							
***Nyctophilus bifax* Thomas, 1915**	Herberton, Qld	x		x				
Nyctophilus daedalus, Thomas 1915	Daly River, NT							
***Nyctophilus walkeri* Thomas 1892**	Adelaide River, NT	x						
***Nyctophilus microtis* Thomas, 1888**	Sogeri, PNG			x				
Nyctophilus microtis bicolor Thomas, 1915	Aroa River, PNG							
Lamingtona lophorhina McKean & Calaby, 1968	Mt Lamington, PNG							
***Nyctophilus microdon* Laurie & Hill, 1954**	Welya, PNG			x				
***Nyctophilus arnhemensis* Johnson, 1959**	Cape Arnhem Peninsula, NT	x						
***Nyctophilus howensis* McKean 1975**	Lord Howe Island							x
***Nyctophilus heran* Kitchener *et al.*, 1991**	Lembata Island, Indonesia					x		
***Nyctophilus nebulosus* Parnaby, 2002**	Noumea, New Caledonia						x	

been used in species diagnoses. The principal characters used to define species include general body size, usually expressed as forearm length; overall body fur colour; extent of development and morphology of a dorsal rostral protuberance posterior to the noseleaf; relative ear size; baculum shape, particularly whether the distal tip forms a solid point or is bifid, and the extent of bifurcation; general skull shape, such as relative proportions and robustness; relative size of the auditory bulla, and relative size of the teeth, especially the extent of reduction of the third molars.

In addition to the above-mentioned limitations in determining species within the genus, or perhaps because of them, most workers (Thomas 1915 being a notable exception) have failed to appreciate the significance of the frequently subtle morphological differences that now appear to be useful guides to species boundaries within the genus. The consequent tendency to synonymise nyctophiline taxa has hindered unraveling species limits by significantly underestimating species diversity within the genus.

A review of the taxonomy of *timoriensis* requires principal consideration of the following named forms of *Nyctophilus*: *major*, *gouldi*, *sherrini* and *howensis*. Consideration of *N. daedalus* Thomas 1915 is also necessary. This taxon was usually treated as the western subspecies of *N. bifax* Thomas, 1915, following Johnson (1964), who synonymised *daedalus* with *bifax*, though without discussion. The status of *daedalus* has ranged from a full species prior to Tate (1941), who suspected that *daedalus* and *bifax* might be subspecifically distinct, and the contemporary recognition of *daedalus* as the western subspecies of *N. bifax*. However, a number of authors have suspected that *daedalus* and *bifax* might not be conspecific (Allison 1982, 1983; Parnaby 1987) and Troughton (1941 and subsequent editions) considered that *daedalus* might be synonymous with *N. gouldi* (as *N. timoriensis gouldi*). Koopman (1984) considered *daedalus*, *bifax* and *gouldi* to be subspecifically distinct but additional material reported by Parnaby (1987) clearly indicated that *N. gouldi* and *N. bifax* were distinct species with extensive sympatry. During the course of this study, a number of large, pale-furred *Nyctophilus* were examined from north-western Queensland and northern Northern Territory. It was initially unclear whether these specimens were large *N. daedalus*, a pale northern form of *N. timoriensis*, or perhaps a large northern form of *N. gouldi*.

The primary focus of this paper is to clarify species limits within the suite of taxa variously associated with the name *timoriensis*. This involves consideration of *timoriensis* itself, and of *major*, *gouldi*, *sherrini*, *daedalus*, *bifax*, *howensis*, and New Guinea material previously referred to *N. timoriensis*.

Methods

Specimen registration prefixes refer to collections held by the following institutions: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; BBM, Bernice P. Bishop Museum, Honolulu; NHM, Natural History Museum, London; C, Museum of Victoria, Melbourne; CG, Muséum National d'Histoire Naturelle, Paris; CM, CSIRO National Wildlife Collection, Canberra; J, JM, Queensland Museum, Brisbane; MG, Museo Civico di Storia Naturale di Genova "Giacomo Doria", Genova, Italy; NTM, Northern Territory Museum and Art Gallery, Darwin; SAM, South Australian Museum, Adelaide; QV, Queen Victoria Museum and Art Gallery, Launceston; WAM, Western Australian Museum, Perth.

The manner is which measurements were taken is shown in Fig. 1 and their abbreviations used in the text are:

CON – Condylobasal Skull Length: from the posterior surface of the occipital condyles to the most anterior extension of the premaxilla;

GL – Greatest length of skull: from the most anterior extension of the premaxilla to the posterior of the lambdoidal crest;

CM^3 – Length of maxillary tooth row: from anterior cingulum of canine to posterior cingulum of M^3;

C^1–C^1 – Outer breadth across canines from cingula;

ZYG – Zygomatic breadth, maximum breadth across zygomatic arches;

INT – Least inter-temporal breadth;

M^3–M^3 – Maximum breadth from left M^3 to right M^3, from labial cingula;

BRH – Braincase height: calliper blade positioned along basioccipital-basisphenoid bones and along the sagittal crest;

MAS – maximum breadth across mastoids;

BTB – Least inter-bulla distance, least distance between each bulla;

BUL – Bulla length, from base of eustachian tube when present;

BAS – Length of basicranial floor: most anterior point of foramen magnum to most anterior point of interpterygoid fossa;

M^3L – M^3 length measured at cingula;

M^3B – maximum breadth of M^3 measured at cingula;

PAL – Palatal-sinual length, from the most posterior extension of the anterior palatial emargination to the most anterior extension of the pterygoid fossa;

MESO – maximum internal breadth of mesopterygoid fossa level with the hamular processes;

JWL – length of right dentary from anterior cingulum of canine to posterior of mandibular condyle;

CM_3 – length of tooth row from anterior cingulum of canine to posterior cingulum of M_3;

M_1-M_3 – length of molar row from anterior cingulum of M_1 to posterior cingulum of M_3;

Baculum Length – maximum length from most posterior tip of proximal arms to distal tip, taken perpendicular to the dorsal surface of the main shaft;

Baculum Breadth – maximum breadth across proximal arms at their base;

Baculum Height – maximum height from ventral extent of proximal arm to distal tip;

Ear Length – taken from the junction of outer ear margin near the jaw;

FA – forearm length, taken with the wings folded;

D1 – Digit 1 length to base of claw;

D3.1 – Digit 3 metacarpal length, from the anterior margin of the forearm to the middle of the joint, taken with the wings half folded;

D3.2 – Length of the first phalanx of third digit;

D3.3 – Length of the second phalanx of third digit;

D5.1 – Digit 5 metacarpal length, from the anterior margin of the forearm to the middle of the joint, taken with the wings half folded;

D5.2 – Length of the first phalanx of fifth digit;

D5.3 – Length of the second phalanx of fifth digit;

HL – Hindleg length, taken with the leg bent and pes bent, note that this is not equivalent to tibia length.

External measurements were taken with a vernier dial calliper to the nearest 0.1 mm. Skull and dental measurements were recorded to the nearest 0.01 mm, except for BUL, BTB, BAS, M^3L and M^3B which were estimated to the nearest 0.01 mm using an eye piece graticule of a dissecting microscope.

CT scans were made using a Skyscan model 1174 micro CT scanner, using the following software packages: NRecon (version 1.5.1.5 (C) Skyscan, Belgium 2008) was used for reconstruction of 3D data sets from RAW CT x-ray images; 3D surface models used in illustrations were generated using CTAn Software (version 1.9.2.3 (C), Skyscan, Belgium 2003-8), and measurements of selected bacula were made using DataViewer (version 1.4.0.4 (C) Skyscan Belgium).

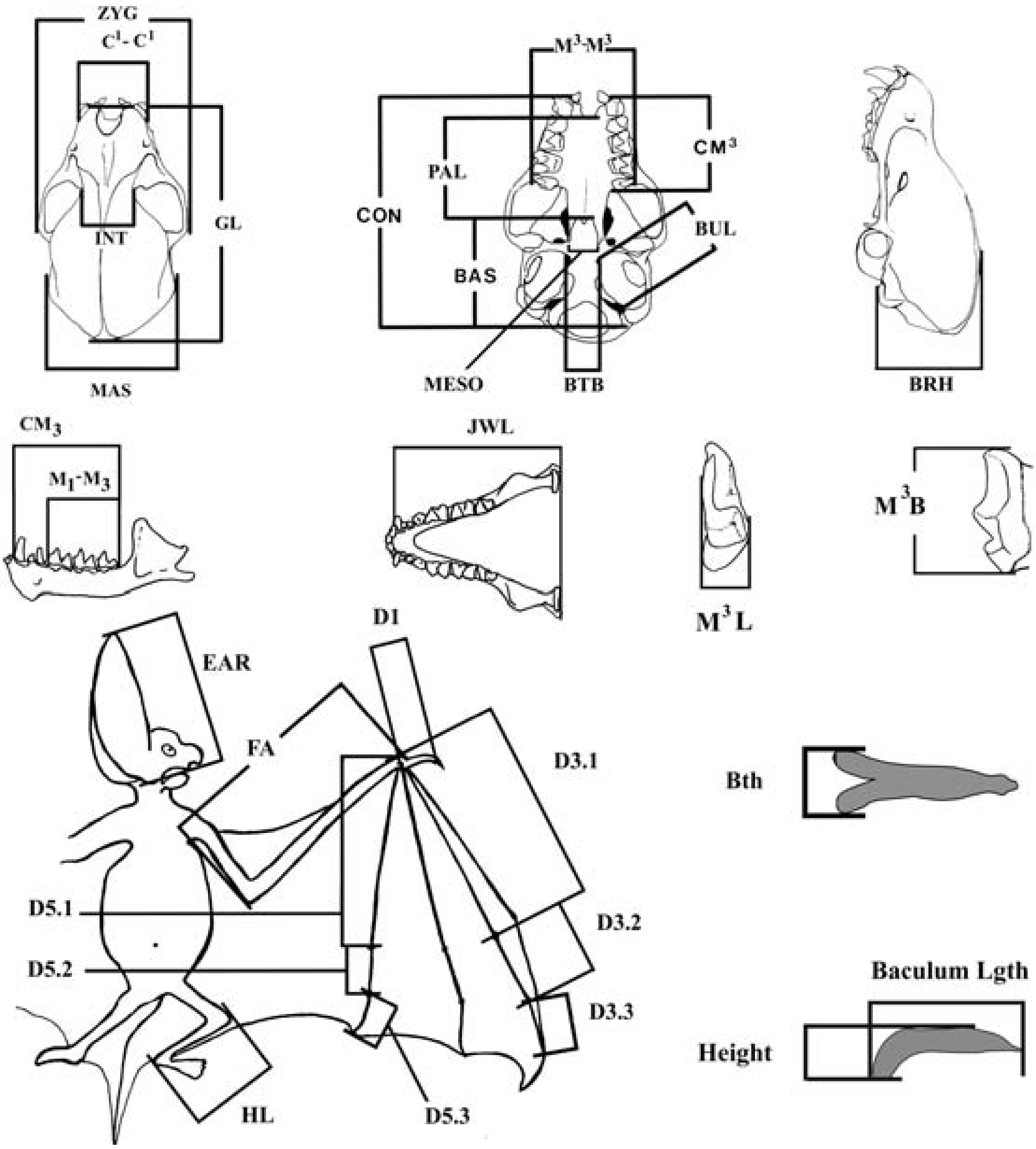


Figure 1. The way in which measurements were taken for cranial, dental, external and bacular characters, see text for abbreviations.

Dental nomenclature follows Menu (1985).

Statistical analyses were undertaken using SYSTAT version 9.0. Canonical Variates Analysis (CVA) and Principal Components Analysis (PCA) were used to explore relationships between specimens, based on untransformed external, skull and dental measurements using a correlation matrix to remove the influence of scale in measurements (Lattin *et al.* 2003). Forearm measurements were combined with craniodental measurements in CVA and PC analyses, partly to increase sample sizes, and because contrasts between skull dimensions and forearm length were known to be diagnostic for some *Nyctophilus* species. An exploratory data analytic approach was taken which does not entail tests of statistical significance.

RESULTS

The status of *Vespertilio timoriensis* Geoffroy, 1806

Geoffroy (1806) established *Vespertilio timoriensis*, the first *Nyctophilus* to be named, on material collected by Peron and Lesueur during the Baudin Expedition of 1800–1804. Geoffroy's description, paraphrased below, is brief:

> *"Vesp. timoriensis. A new species which we owe to the work and research of Peron and Lesueur. The ears are large, of the length of the head, and are united together by a small membrane, the tragus is shaped like a half heart. The fur is brownish black above, ashy brown underneath; the hairs are very bushy, fairly long and soft; its measurements are: body 70 mm; tail 40 mm and wingspan 270 mm."*

Plate 47 accompanying his description illustrates the bust of a long-eared bat that is consistent with a species of *Nyctophilus*, particularly in the characteristic tragus shape.

Authors in the decades following Geoffroy (1806) mostly paraphrased his original account and state that the species was from Timor (Desmarest 1820, Lesson 1827, Fischer 1829, Geoffroy 1832). Temminck (1840), in what appears to be a first hand communication from Geoffroy, notes that it is uncertain whether *timoriensis* originated from South Africa, Asia or Australia.

Geoffroy gave no indication of the number of specimens upon which his description is based although it is generally assumed to be a single specimen (Tomes 1858, Thomas 1914, Tate 1941). However, Temminck (1840) states that, according to Geoffroy, the species was known from two specimens, a male and female, that closely resembled each other.

Two specimens in the Muséum National d'Histoire Naturelle, Paris have been suspected, at different times, of being Geoffroy's original material and thus possible syntypes of *timoriensis*. Rode (1941) listed no. 884 (now registered as CG1990-36), a puppet skin with skull extracted and lost, as the type. Tate (1941) based his account of *N. timoriensis* on a then unregistered male in alcohol, skull extracted and evidently without locality or details of collector (now registered as CG1985-33). In 1990 I examined both specimens, through the kindness of Michel Tranier. Neither specimen is likely to be among the original material upon which Geoffroy based his description.

The specimen CG1990–36 has long ears which are joined in the midline and has a noseleaf that resembles that of *Nyctophilus*. However, it differs from any *Nyctophilus* that I have examined in that both surfaces of the ears, snout and nose-leaf are covered by short thick hairs, unlike the fine hairs of any species of *Nyctophilus*. Furthermore, tragus shape of CG1990–36 differs from all *Nyctophilus* in being sharply inflected midway along its length. The wingspan of this specimen is 264mm but as the left wing tip is missing, wingspan could have been around 270mm as given in the original description of *timoriensis*; Tail length is about 40mm and snout-vent length is 53mm, though the snout is slightly bent. Ear length is 19mm though the ear tip is slightly curled. Thus if body length included ears, then body length would equate to about 70mm. Although these dimensions correspond approximately with those given by Geoffroy for *Vespertilio timoriensis*, this specimen is unlikely to have formed the basis of Geoffroy's description because its tragus shape is distinctly unlike that shown in his illustration. Overall, I am not convinced that this specimen is a *Nyctophilus* and further examination is warranted to clarify its identity, including direct comparisons with material of other long-eared vespertilionid genera. Irrespective of its identity, there is no certainty that the specimen represents Geoffroy's original material, as discussed below.

Specimen CG1985-33, suspected by Tate (1941) to be a syntype of *Vespertilio timoriensis*, is identifiable on morphological criteria as a specimen of *N. sherrini* from Tasmania, recognised here as a full species (see below). In its size (see Table 9), elongate skull and unreduced third molars, this specimen equates with *N. sherrini* but differs from all other large mainland Australian forms of the genus. *Nyctophilus sherrini* has the most distinctive skull morphology of any of the large extant forms of the genus in its combination of relatively narrow skull, broad intertemporal region, unreduced third molars, short interpterygoid fossa, and elongate posterior extension of the palate. In all of these features, CG1985-33 differs substantially from the holotype male of *N. major*, but resembles the young adult male holotype of *N. sherrini* (Fig. 2). Michel Tranier (*in lit.*, 3 May, 1990) has established that this specimen was collected in Tasmania and acquired by the Paris Museum in 1840: "probably from Gould collection, and maybe as material given to Verreaux". Tranier further stated that "I have reviewed our specimens of *Nyctophilus*: I am sure that the only type is No. 884…I am afraid that the exact origin of *N. timoriensis* will never be elucidated".

Thomas (1914) considered that the name *timoriensis* should be "dropped for the present, as it is impossible to identify it with certainty among the Australian species, and it may yet turn up in Timor." He proposed that *N. major* Gray, 1875 be used instead of *N. timoriensis* with reference to populations from Western Australia, and promoted this approach in his generic revision (Thomas

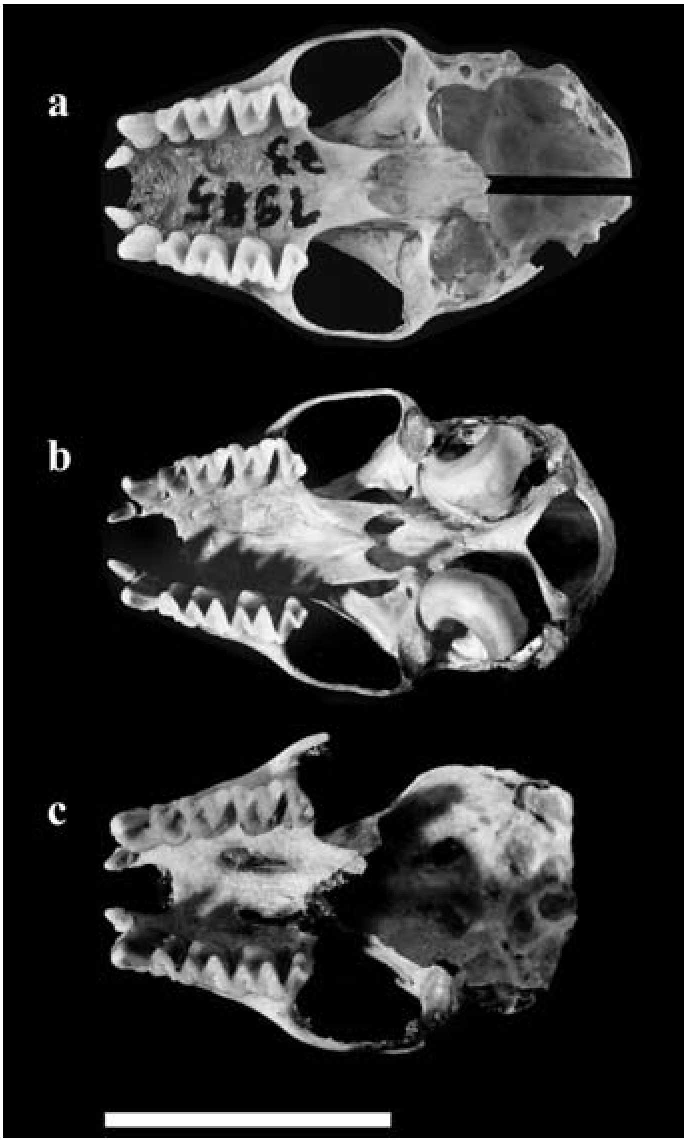


Figure 2. Photographs of the ventral views of the skull of a), CG1985-33, a putative syntype of *Vespertilio timoriensis* Geoffroy, 1806; b), holotype of *N. sherrini* and c), holotype of *N. major*. All are males. Scale bar represents 10 mm. [Photographs b and c, courtesy of the Natural History Museum, London.]

1915). As detailed above, I also believe that it is not possible to determine which species formed the basis of Geoffroy's original description and illustration. Moreover, even if the species identity of the skin CG1990-36 (No. 884) could be determined (e.g. through DNA sequence analysis), it remains uncertain as to whether this specimen is a syntype, given that tragus shape is inconsistent with Geoffroy's illustration.

The principal justification for prior application of *timoriensis* to Australian *Nyctophilus*, the perception that *Nyctophilus* does not occur in Timor, and therefore must have come from an Australian locality (Tomes 1858; Iredale and Troughton 1934; Goodwin 1979), became invalid with the description of *N. heran* from eastern Indonesia (Kitchener *et al.* 1991; Corbet and Hill 1992). Even more immediately, specimens of a *Nyctophilus* were recently obtained from Timor by Kristopher Helgen (pers. comm.).

Stability of nomenclature is a central tenet of the International Code of Zoological Nomenclature (ICZN 1999). The confused use of *timoriensis* and *major* for Western Australian populations since 1981 has culminated in the southwestern populations being listed by McKenzie (2008) as "*Nyctophilus* sp." in the influential text of Van Dyck and Strahan (2008).

For the present, I follow the opinion of Thomas (1914) and treat *Vespertilio timoriensis* Geoffroy, 1806 as a *nomen dubium*, based on the level of uncertainty surrounding the whereabouts of Geoffroy's material, uncertainty over the type locality, and the improbability of matching any current taxon to Geoffroy's description. A more formal action to stabilize usage of the name *V. timoriensis* Geoffroy, 1806 for the recently (re)discovered Timorese *Nyctophilus* will be taken in a separate publication. This will require comparison with *N. heran* from nearby Lembata Island, to which the Timorese material bears a general resemblance.

The nomenclatural history of *timoriensis* and associated taxa

In the first revision of *Nyctophilus*, Tomes (1858) questioned the accuracy of the type locality of *timoriensis* evidently on the grounds that further specimens had not been obtained from Timor, despite extensive collections of bats having been made, and because he examined the "original specimen" of Geoffroy which he considered to be "absolutely identical" with three collected for John Gould from southwestern Western Australia. Tomes did not mention Gray's (1844-1875) application of the name *N. major* to a specimen from southwestern Western Australia. Gray (1844-1875) stated that he applied the name *N. major* to a large specimen of the genus from Western Australia, because he was unable to allocate it to any of the four species recognised in the revision of Tomes (1858). Gray (loc. cit.) referred to a colour plate of this specimen but did not provide a description or measurements of the holotype. Peters (1861) noted that *N. major* was not mentioned by Tomes (1858) and thus omitted from the synonomy of *N. timoriensis*. Thomas (1914) drew attention to the fact that, because the colour plate of *N. major* was not published by Gray until 1875, authorship should be accredited to Peters, 1861 and not Gray, 1875. However, Mahoney and Walton (1988) established the publication date of Gray's plate as 1844, on the basis that, although Gray's plate and text were published progressively in parts until completion in 1875, Gray had publicly distributed the plate at various times from 1844.

In his review of *Nyctophilus*, Dobson (1878) synonymised the four species recognised by Tomes (1858), i.e. *N. geoffroyi* Leach, 1821, *N. unicolor* Tomes, 1858 and *N. gouldi*, with *timoriensis*. He believed that the slight differences used by Tomes to differentiate species were most likely age or geographic differences and in view of the limited material, felt that recognition of more than a single species was unjustified. Dobson's proposal was rejected by Thomas (1914) who followed the species arrangement of Tomes. Thomas suggested that *major* Peters, 1861 be used for large *Nyctophilus* from

southwestern Western Australia and that *timoriensis* be dropped due to the uncertainty surrounding the identity of Geoffroy's type(s) among specimens in the Paris Museum as well as the uncertainty about the type locality. In his revision, Thomas (1915) recognised *major* and *gouldi* as separate species and described as new, *N. sherrini* from Tasmania, *N. daedalus* from the Northern Territory and *N. bifax* from Queensland.

Iredale and Troughton (1934) considered Geoffroy's (1806) identification of Timor as the type locality of *Vespertilio timoriensis* to be erroneous. They regarded the type locality to be southwestern Western Australia and populations from that region to represent nominate *timoriensis*, with *major* as a junior synonym. They treated *gouldi* and *sherrini* as subspecies of *N. timoriensis*, from southeastern mainland Australia and Tasmania, respectively.

In his generic review, Tate (1941) recognised a *timoriensis* group consisting of the forms *major*, *gouldi*, *sherrini* and *timoriensis*. Tate based his concept of *timoriensis* on an unregistered spirit specimen in the Paris Museum which he suspected was Geoffroy's original specimen (now CG1985-33; argued above to be a specimen of *N. sherrini*, probably collected well after Geoffroy's publication). Tate noted differences in the skull and dentition between the holotype of *major* and the presumed holotype of *N. timoriensis*. In his 1941 treatment, he appears to have regarded *gouldi* and *sherrini* as races of *N. timoriensis*. However, in a subsequent work, Tate (1952) listed *major* and *sherrini* as subspecies of *N. timoriensis* and *N. gouldi* as a distinct, albeit closely related, species.

Through much of the second half of the 20th Century, only two species of *Nyctophilus* were recognized in the southern half of Australia: *N. geoffroyi* and *N. timoriensis* (e.g. Troughton 1967; Ride 1970; Corbet and Hill 1980; Allison and Koopman in Honacki *et al.* 1982). Hall and Richards (1979) provided evidence that *N. gouldi* and *N. timoriensis* are distinct species and summarised the distribution of each species in eastern Australia. Prior to this, Tate (1941) had been universally followed in treating *gouldi* as the southeastern Australian race of *timoriensis*; apparently, his revised opinion, that *N. gouldi* was a separate species (Tate 1952), had been overlooked. The presence of *N. gouldi* in far southwestern Western Australia was first noted by Kitchener and Vicker (1981).

Most authors subsequent to Tate (1952) have treated *major* as a synonym of *N. timoriensis* (Troughton 1967; Ride 1970; Corbet and Hill 1980; Allison and Koopman in Honacki *et al.* 1982; Richards 1983; Parnaby 1995; Churchill 1998; Simons 2005; ABRS 2008). Kitchener and Vicker (1981) used *N. major* for Western Australian populations, though without comment. Subsequent confusion has arisen regarding Western Australian populations which have been variously called *N. major* (e.g. McKenzie and Robinson 1987; Hosken 1996; Bailey and Haythornthwaite 1998; Hobbs *et al.* 2003), *N. timoriensis major* (e.g. Hosken 1997; Menkhorst and Knight 2004) or *N. timoriensis* (e.g. How *et al*. 2001; Bullen and McKenzie 2004).

The more recent assessments of *Nyctophilus* offer divergent arrangements of the *timoriensis* group. Corbet and Hill (1980, 1986) recognise *N. timoriensis* alone. Hill and Koopman (1981) and Allison (1982) tentatively recognise *N. timoriensis* and *N. gouldi* as full species. Hill and Pratt (1981) recognised *major* and *timoriensis* as separate taxa but reserved judgement on whether the differences warranted subspecies or full species rank. They restricted nominate *N. timoriensis* to a possible Timorese population. Koopman (1984) presents the most recent published revision of Australian *Nyctophilus*. He treated *N. gouldi* as a distinct species and recognised three subspecies of *timoriensis* in Australia: *major* from southwestern Western Australia; *sherrini* from Tasmania; and tentatively referred two specimens from northern Australia to nominate *timoriensis*.

In summary, all authors except Thomas (1915) have applied *timoriensis* to at least some eastern Australian *Nyctophilus* populations and have referred Western Australian populations either to nominate *N. timoriensis*, *N. major* or to *N. timoriensis major*. Two other taxa have been treated as subspecies of *N. timoriensis* by many authors in the past: *gouldi* from southeastern Australia and *sherrini* from Tasmania, with Thomas (1915) alone recognising both as full species.

As noted above, Koopman (1984) identified possible nominate *N. timoriensis* within the northern Australian bat fauna. At the same time, he expressed the opinion that two other northern nyctophiline taxa, *bifax* and *daedalus*, could be subspecies of *N. gouldi* (Koopman 1984). In this, he partly reflected Troughton's (1941) opinion that *daedalus* from northern Australia might be synonymous with *N. gouldi* (as *N. timoriensis gouldi*) from south-eastern Australia.

In his original description of the species, Thomas (1915) compared *N. daedalus* with *N. gouldi* and *N. bifax*. Diagnostic criteria listed by Thomas for separating *N. daedalus* from *N. gouldi* are the smaller bullae, shorter ears and a less developed nasal prominence. The only character cited as distinguishing *N. daedalus* from *N. bifax* is baculum shape: the distal tip forms a solid point in *N. daedalus* but a distinct notch in *N. bifax*. Tate (1941, 1952) was ambivalent about the relationship between the two taxa. In 1941 he noted the consistently greater Zygomatic Breadth and more reduced M^3 of *N. daedalus*. However, he also noted an overall similarity between *daedalus* and *N. bifax* and concluded that they might be subspecies. After examining more specimens of *N. bifax*, Tate (1952) was able to confirm a consistent difference in baculum shape, as noted initially by Thomas. His comments suggest that he now regarded them as possibly distinct species.

Johnson (1964) treated *daedalus* as a western, allopatric subspecies of the eastern Australian *N. bifax* and most authors over the past four decades have followed this opinion (e.g. Ride 1970, Hall and Richards 1979, Corbet and Hill 1986, Allison 1983). However, Johnson (1964) did not justify his treatment of *daedalus*, which is at odds with the views expressed by the majority of preceding workers (Iredale and Troughton 1934, Troughton 1941 and subsequent editions, Tate 1941 and 1952, Johnson 1959).

As noted above, Troughton (1941) speculated that *daedalus* might prove to be a subspecies of *N. gouldi* from southeastern Australia. This view was extended by Koopman (1984) who tentatively synonymised both *daedalus* and *bifax* with southeastern Australian *N. gouldi*, suggesting that *daedalus* was in some respects morphologically intermediate between *gouldi* and *bifax*. However, Allison (1982, 1983) noted the uncertain status of *daedalus* and speculated that it could represent a separate species on the basis of baculum differences, as did Parnaby (1987).

Hill and Pratt (1981) report two large specimens of *Nyctophilus* (an adult male and female) from Mt Missim, northeastern Papua New Guinea which they provisionally refer to *N. timoriensis*. They examined the skull of the female specimen, of which I have examined photographs. I have obtained a further three adult female specimens from Mt Missim, which appear to be conspecific with those reported by Hill and Pratt.

Systematics

Nyctophilus corbeni sp. nov.

Holotype: Australian Museum number M38833 adult male, field number 6HP04, body fixed in 80% ethanol and stored in 75% ethanol, skull extracted, penis separated from the body and stored in 75% ethanol. Captured by H. Parnaby on 7th May 2006 in a bat trap (harp trap) set across a road. Field numbers for vials of tissue samples preserved in 90% ethanol at the Australian Museum are: liver, 39810; 39856; pectoral muscle: 39729, 39764. Measurements of the holotype are given in Table 2.

Paratypes: A total of four, all captured by H. Parnaby in bat traps set across roads on 7th May 2006: AM registration numbers, field numbers in brackets: AM38834 (6HP05), adult female captured at the type locality, field number for liver sample stored in 90% ethanol is 39779; the remaining three paratypes

Table 2. Cranial and external measurements of holotypes of *N. major* and associated forms. Measurements taken from Thomas (1915), Tate (1941), J.E. Hill (*pers. comm.*) and Glenn Hoye (*pers. comm.*).

	N. major	*N. m. tor* subsp. nov.	*N. corbeni* sp. nov.	*N. sherrini*	*N. daedalus*
Skull and dental measurements	NHM 44.7.9.20 male	WAM63601 male	AM38833 male	NHM 52.1.15.50 male	NHM 97.4.12.8 male
GL	18.0	18.1	19.43	18.5	17.6
CON		16.51	17.75	17.2	16
CM^3	7.3	6.60	6.90	6.9	6.4
C^1–C^1	5.9	5.41	6.01	4.7	5.2
ZYG	12	11.42	12.45	11.4	11.4
INT	3.8	3.70	3.83	4.0	3.7
M^3-M^3	7.9	7.30	7.97	7.1	7.35
M^3L	0.89	0.70	0.75	0.84	0.62
M^3B	2.05	1.95	2.15	2.2	1.8
BRH		6.38	7.14	6.35	6.5
MAS		9.80	10.25	8.9	9.2
BUL		4.05	4.3	4.2	3.7
BTB		1.80	2.1		
BAS		6.4	7.3		
PAL		6.6	6.3	7.1	6.6
MESO		1.95	2.0	2.0	1.8
JWL		11.95	13.3		
CM_3		7.25	7.64		
M_1-M_3		5.1	5.15		
External measurements					
Ear length		27.1*	25.2*		
Forearm length	44	41.5*	45.4*	45	41
Digit 1 length		6.2	6.4		
Digit 3 metacarpal length		39.5	44.2		
Digit 3 phalanx 1 length		15.6	16.7		
Digit 3 phalanx 2 length		14.6	15.2		
Digit 3 phalanx 3 length		9.1	10.3		
Digit 5 metacarpal length		38.3	41.6		
Digit 5 phalanx 1 length		10.8	11.5		
Digit 5 phalanx 2 length		9.3	9.7		
Hind-leg length		21.0	21.4*		
HB	65	51	59*	55	52
Tail	40	42	54*	45	41
Weight		11*	13.5*		

* field measurements.

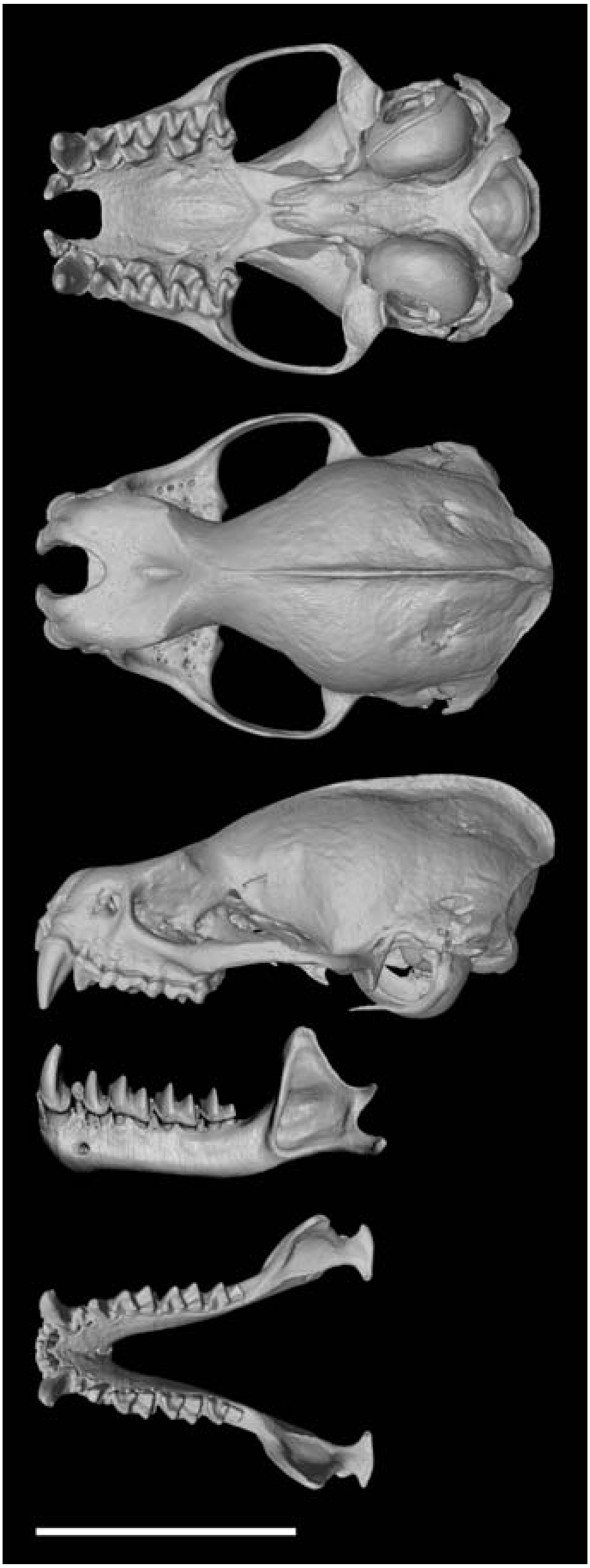


Figure 3. X-ray CT scans of the holotype skull of *N. corbeni* **sp. nov.**, adult male AM38833. Scale bar represents 10 mm.

were captured at a site on Old Coghill Track, 0.6 km west of junction with track to main Gilgai Waterhole (30° 29' 51"S, 149° 20' 01"E, altitude approximately 215m), Pilliga East State Forest, New South Wales: AM38831 (6HP02) adult male, skull extracted, field numbers for tissue samples stored in 90% ethanol are Liver (39820, 39868) and pectoral muscle (39811); AM38832 (6HP03) adult male, field number for liver sample stored in 90% ethanol is 39846; and AM38835 (6HP06) adult male, field number for liver sample stored in 90% ethanol is 39840. Bodies of all four paratypes were fixed in 80% ethanol and stored in 75% ethanol. Tissue samples for all four specimens are held at the Australian Museum.

Type Locality: Old Coghill Track, 0.7 km east of junction with track to main Gilgai Waterhole; formerly Gilgai Flora Reserve, Pilliga East State Forest, New South Wales. Approximate altitude 235 m. Coordinates obtained from a Garmin GPS are 30° 29' 58"S, 149° 20' 53"E.

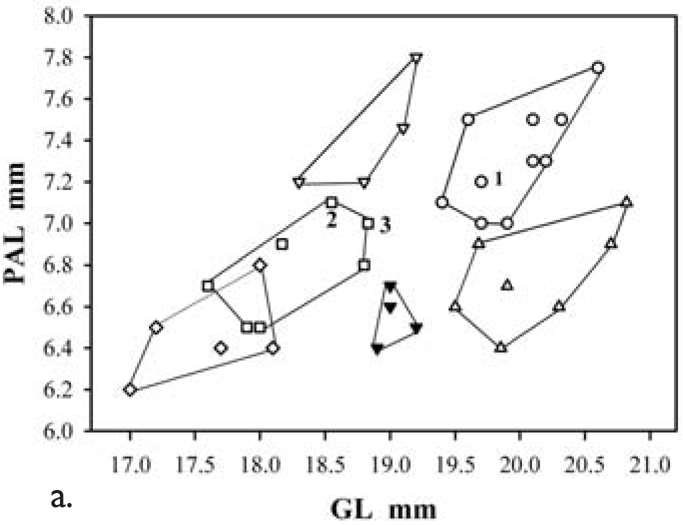
Diagnosis: A large species similar in body and skull size to nominotypical *N. major* but differing in: having a relatively broader and more robust skull: broader braincase; more expanded and rounded zygomatic arches; a more truncated rostrum (compare Figs. 3 and 10); palate shorter relative to skull length (Fig. 4 and Table 4); baculum usually > 4.6 mm (Fig. 5 and 6, Table 3).

It differs from *N. sherrini* in: it has a relatively much broader and more robust skull; more massive and relatively broader rostrum; relatively narrower INT; relatively shorter palate (Fig. 4); metacone absent on M^3 and distinctly more reduced third molars (Fig. 7); and relatively smaller bullae.

It differs from *N. gouldi* in: it has a broader, far more robust skull; more massive rostrum; relatively smaller bullae; relatively narrower INT; C^1–C^1 > 5.5 mm (n = 125); ZYG > 11.1 mm (n = 125); more reduced third molars, metacone absent and premetacrista nearly obsolete; a longer baculum (> 3.7 mm) with a more slender shaft (Fig. 5); and conspicuously larger body size in sympatry with *N. gouldi*: FA > 42.0 mm (females) or 41.0 mm (males); C^1–C^1 > 5.0 mm.

It differs from *N. nebulosus* in: paler overall fur colour; larger skull and dental dimensions; more robust skull; PAL shorter relative to GL; far greater reduction of third molars, metacone absent and third commissure obsolete rather than well developed and subequal to second commissure; baculum larger (> 4.0 mm) with thinner shaft (compare Fig. 5 with Fig. 4 of Parnaby 2002).

It differs from *N. daedalus* in: averaging larger for all external and cranial dimensions (Tables 3 and 4); C^1–C^1 > 5.6 mm; PAL relatively shorter and BAS relatively longer, BAS > 6.5 mm; bullae relatively larger and BUL > 3.9 mm; protocone of M^1 and M^2 less reduced resulting in a convex rather than truncated lingual margin; baculum longer with a relatively narrower base and more slender shaft (Fig. 5), baculum length > 4.0 mm (Table 3).



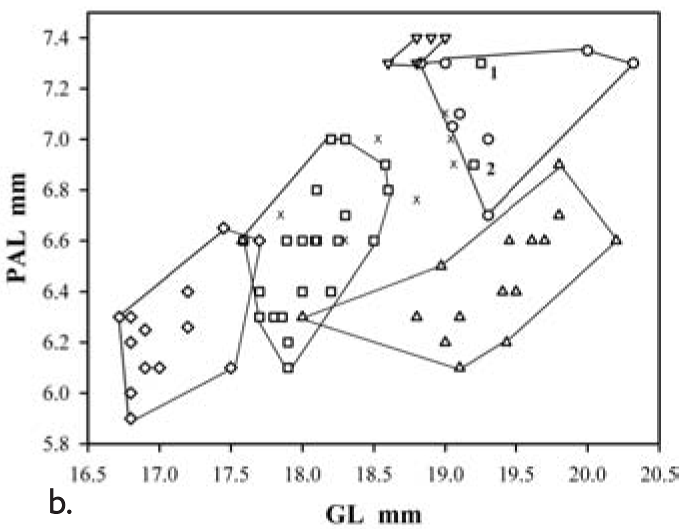


Figure 4. Plot of PAL vs GL for *N. major* complex. **a)** adult females: 1, specimen from Mundrabilla (WAM22953); 2, Katanning (AMNH197281); 3, Woodanilling (AM37642); **b)**, adult males, 1, specimen from Balladonia (AM39802); 2, specimen from Madura (WAM28398); X = unallocated adults from Dryandra Woodlands. Species symbols are: *N. corbeni* **sp. nov.** (△), *N. major major* (○), *N. m. tor* **subsp. nov.** (□), *N. sherrini* (∇), *N. daedalus* (◊) and *N. shirleyae* **sp. nov.** (▼).

Easily distinguished from *N. howensis* which has a much larger skull: GL, 23.09 vs 20.82; ZYG 13.88 vs 13.2; C¹–C¹ (outer alveoli), 6.7 vs 6.5 (outer cingula); BRH 7.4 vs 7.45; INT 4.23 vs 4.04; CM³ 8.1 vs 7.4; M³-M³ (outer alveoli) 8.71 vs 8.5 (outer cingula); MAS estimated at 11.3 vs 11.0; PAL, 9.46 vs 7.1; BAS 7.57 vs 7.71. *N. howensis* has a relatively much narrower and more gracile skull (compare Figs 3 and 29): relatively narrower ZYG and rostrum, and narrower more elongate braincase; relatively narrower anterior palatal emargination, rostral sulcus and mesopterygoid fossa; relatively longer PAL; and M³ less reduced: the metacone is clearly present.

Table 3. Summary statistics for bacula of various *Nyctophilus* species.

	Mean	s.d.	Range	N
Baculum Length				
N. corbeni sp. nov.	4.97	0.372	4.54–5.73	11
N. major	4.46	0.124	4.30–4.57	4
N. m. tor subsp. nov.	4.38	0.136	4.18–4.59	12
N. sherrini	4.32	0.296	4.00–4.51	3
N. gouldi	3.26	0.159	2.99–3.69	26
N. daedalus	3.50	0.237	3.20–3.85	6
N. nebulosus			2.95	1
N. bifax	3.49	0.129	3.28–3.73	10
Baculum Breadth				
N. corbeni sp. nov.	1.24	0.194	0.78–1.46	10
N. major	1.27	0.039	1.23–1.31	3
N. m. tor subsp. nov.	1.18	0.064	1.07–1.31	11
N. sherrini	1.28	0.089	1.18–1.35	3
N. gouldi	1.09	0.090	0.90–1.27	26
N. daedalus	1.16	0.074	1.07–1.23	5
N. nebulosus			1.11	1
N. bifax	1.21	0.105	1.07–1.39	9
Baculum Height				
N. corbeni sp. nov.	1.69	0.218	1.44–2.09	11
N. major	1.35	0.294	1.02–1.60	3
N. m. tor subsp. nov.	1.42	0.106	1.23–1.60	11
N. sherrini	1.48	0.142	1.37–1.64	3
N. gouldi	1.06	0.119	0.86–1.35	26
N. daedalus	1.24	0.061	1.15–1.31	5
N. nebulosus			–	
N. bifax	1.24	0.111	1.07–1.43	10

It differs from *N. heran*, which has a better developed postnasal bump, more pronounced membrane uniting the distal median sides of the paired post-nasal prominences, and in being larger for most measurements (comparisons are for adult males): e.g. GL > 18.0 mm vs < 17.0 mm; C¹–C¹ > 5.7 mm vs 4.5 mm; in having relatively much smaller bullae; baculum larger, baculum length > 4.0 mm, with relatively smaller basal arms and main shaft tapers less to distal point (compare Fig. 5 with Fig. 5 of Kitchener *et al.* 1991).

Easily distinguished from *N. geoffroyi* in: having a simpler post-nasal elevation which has a simple median vertical grove, rather than an more developed pair of mounds joining in the distal mid-line by an elastic membrane which forms a distinctive "Y"-shaped structure; by larger size, e.g. compared to sympatric *N. geoffroyi*, GL > 18.0 mm vs ≤ 16.7 mm (n = 126, sexes combined for mainland *N. geoffroyi*); C¹–C¹ > 5.6 mm vs ≤ 4.8 mm (n = 117) relatively smaller bullae; skull far more robust; more reduced M¹ protocone such that lingual margin is truncated rather than convex; M³ more reduced with more rudimentary third commissure and metacone not present; distal tip of glans penis blunt and rounded rather than forming an elongate "beak", lacking a

Table 4. Summary statistics for 11 external and 15 skull and dental dimensions of adult specimens examined of *N. corbeni* **sp. nov.**, *N. major major*, *N. major tor* **subsp. nov.** and *N. daedalus*.

N. corbeni sp. nov.

	Female						Male					
	Mean	s.d.	Min	Max	N	CV	Mean	s.d.	Min	Max	N	CV
EAR	26.40	1.794	24.3	29.3	10	6.8	26.43	1.069	24.4	28.3	26	4.0
D1	7.25	0.446	6.4	7.6	6	6.2	6.48	0.459	5.6	7.2	16	7.1
FA	46.65	1.238	44.7	48.9	14	2.7	44.72	1.669	41.3	49.4	35	3.7
D31	45.96	1.261	44.2	47.6	13	2.7	43.59	1.748	41.2	49.5	28	4.0
D32	18.50	1.072	16.8	20.4	10	5.8	17.03	0.727	16.0	18.3	21	4.3
D33	16.00	0.865	14.6	17.1	8	5.4	15.16	0.654	13.9	16.2	21	4.3
D51	44.95	1.284	43.4	47.1	13	2.9	42.44	1.684	40.1	48.3	29	4.0
D52	12.75	0.845	11.4	14.1	10	6.6	11.50	0.375	10.7	12.1	21	3.3
D53	10.55	0.750	9.3	11.3	6	7.1	9.57	0.875	7.8	11.6	21	9.1
HL	21.96	0.903	20.5	23.6	13	4.1	21.28	0.799	20.0	23.0	29	3.8
WT	16.22	2.055	14.3	20.0	6	12.7	13.52	0.996	11.2	15.5	20	7.4
CON	18.20	0.340	17.80	18.76	10	1.9	17.54	0.420	16.70	18.30	23	2.4
GL	20.11	0.447	19.50	20.82	10	2.2	19.20	0.508	18.00	20.20	23	2.6
CM^3	7.25	0.159	7.00	7.44	10	2.2	6.98	0.211	6.55	7.40	23	3.0
C^1-C^1	6.27	0.155	5.90	6.50	10	2.5	6.06	0.172	5.70	6.50	23	2.8
ZYG	12.77	0.261	12.45	13.20	10	2.0	12.35	0.278	11.90	12.80	22	2.3
INT	3.75	0.145	3.60	4.00	10	3.9	3.74	0.160	3.45	4.04	23	4.3
M^3–M^3	8.22	0.256	7.77	8.50	10	3.1	7.92	0.224	7.50	8.30	23	2.8
BRH	7.16	0.167	6.95	7.45	10	2.3	6.93	0.189	6.60	7.30	23	2.7
MAS	10.59	0.326	9.90	11.00	10	3.1	10.18	0.188	9.90	10.50	23	1.8
BTB	2.26	0.165	1.97	2.50	10	7.3	2.14	0.103	1.97	2.30	21	4.8
BUL	4.42	0.126	4.18	4.60	10	2.9	4.27	0.113	4.10	4.50	21	2.6
BAS	7.42	0.287	6.97	7.71	10	3.9	7.12	0.236	6.70	7.71	21	3.3
M^{3}L	0.87	0.039	0.82	0.90	4	4.5	0.85	0.055	0.78	0.98	10	6.5
M^{3}B	2.41	0.039	2.38	2.46	4	1.6	2.23	0.087	2.09	2.42	10	3.9
PAL	6.74	0.237	6.40	7.10	7	3.5	6.45	0.220	6.10	6.90	15	3.4

N. major major

	Female						Male					
	Mean	s.d.	Min	Max	N	CV	Mean	s.d.	Min	Max	N	CV
EAR	26.22	1.426	24.4	28.6	13	5.4	26.30	0.957	24.7	27.5	6	3.6
D1	6.69	0.553	6.0	7.6	9	8.3	6.93	0.153	6.8	7.1	3	2.2
FA	45.91	1.354	43.5	48.4	19	2.9	44.55	1.584	42.5	47.5	8	3.6
D31	43.84	1.250	42.2	45.9	14	2.9	42.29	1.716	40.05	44.9	6	4.1
D32	17.11	0.651	16.1	17.9	10	3.8	16.52	0.746	15.5	16.6	5	4.5
D33	15.27	0.650	14.2	16.1	10	4.3	15.13	0.643	14.4	15.6	3	4.2
D51	42.68	1.188	40.8	44.7	14	2.8	41.56	1.540	39.8	44.0	6	3.7
D52	11.91	0.415	11.4	12.6	10	3.5	11.46	0.844	10.7	12.5	5	7.4
D53	9.69	0.536	9.1	10.7	10	5.5	9.57	1.007	8.5	10.5	3	
HL	21.96	0.649	21.1	23.2	13	3.0	20.80	0.860	20.2	22.3	5	4.1
WT			15.0	16.5	2				12.0	13.5	2	
CON	18.37	0.394	17.70	19.00	12	2.1	17.87	0.560	17.18	18.89	8	3.1
GL	19.95	0.477	19.10	20.70	12	2.4	19.36	0.523	18.83	20.32	8	2.7
CM^3	7.46	0.230	7.15	7.80	13	3.1	7.27	0.159	7.04	7.55	8	2.2
C^1-C^1	6.05	0.213	5.70	6.35	13	3.5	5.90	0.265	5.70	6.52	8	4.5
ZYG	12.28	0.404	11.70	13.30	13	3.3	11.99	0.384	11.60	12.50	7	3.2
INT	3.83	0.156	3.50	4.00	13	4.1	3.88	0.124	3.71	4.10	8	3.2
M^3–M^3	8.09	0.311	7.70	8.60	13	3.8	7.88	0.216	7.60	8.10	8	2.7
BRH	6.93	0.293	6.50	7.50	12	4.2	6.92	0.093	6.80	7.06	7	1.3
MAS	10.20	0.326	9.70	10.70	12	3.2	10.02	0.300	9.70	10.64	7	3.0
BTB	2.02	0.165	1.89	2.30	8	8.2	1.97	0.083	1.89	2.05	5	4.2
BUL	4.34	0.121	4.18	4.51	10	2.8	4.25	0.071	4.15	4.35	5	1.7
BAS	6.96	0.293	6.60	7.38	9	4.2	6.66	0.351	6.40	7.22	5	5.3
M^{3}L	0.86	0.054	0.78	0.94	6	6.2	0.87	0.047	0.82	0.90	3	5.4
M^{3}B	2.19	0.104	2.05	2.34	6	4.7	2.20	0.085	2.13	2.30	3	3.9
PAL	7.30	0.243	7.00	7.75	11	3.3	7.14	0.222	6.70	7.35	8	3.1

Table 4. continued

N. m. tor subsp. nov.

	Female						Male					
	Mean	s.d.	Min	Max	N	CV	Mean	s.d.	Min	Max	N	CV
EAR	24.23	1.638	21.5	27.5	19	6.8	25.02	1.452	21.3	27.3	43	5.8
D1	6.28	0.364	5.6	6.8	16	5.8	6.16	0.376	5.3	7.0	32	6.1
FA	41.34	1.188	39.3	44.6	26	2.9	40.94	1.347	37.6	43.3	53	3.3
D31	39.84	1.354	37.7	43.0	25	3.4	39.32	1.292	36.8	42.0	53	3.3
D32	15.73	0.760	14.2	17.0	16	4.8	15.46	0.687	13.9	17.0	37	4.4
D33	13.87	0.732	12.7	15.4	16	5.3	13.89	1.256	7.8	15.4	35	9.0
D51	39.11	1.141	36.9	41.6	25	2.9	38.44	1.183	36.4	40.7	52	3.1
D52	11.08	0.672	10.1	12.6	16	6.1	10.87	0.463	9.9	11.7	35	4.3
D53	9.09	1.137	6.1	10.6	16	12.5	9.31	0.605	8.1	10.6	36	6.5
HL	20.68	0.890	19.2	22.5	17	4.3	19.79	0.720	18.4	21.5	43	3.6
WT			11.0	11.5	2		10.82	1.361	8.0	12.3	18	12.6
CON	16.68	0.238	16.20	17.00	12	1.4	16.61	0.314	15.90	17.20	30	1.9
GL	18.06	0.276	17.50	18.30	12	1.5	18.04	0.347	17.20	18.75	31	1.9
CM^3	6.68	0.156	6.40	7.00	12	2.3	6.76	0.163	6.50	7.10	31	2.4
C^1-C^1	5.34	0.218	5.00	5.60	12	4.1	5.39	0.187	5.00	5.70	31	3.5
ZYG	11.25	0.271	10.70	11.60	11	2.4	11.12	0.281	10.50	11.62	31	2.5
INT	3.59	0.089	3.50	3.80	12	2.5	3.65	0.120	3.49	4.00	31	3.3
M^3–M^3	7.36	0.226	7.00	7.80	12	3.1	7.31	0.185	6.90	7.70	31	2.5
BRH	6.31	0.135	6.10	6.60	12	2.1	6.46	0.177	6.10	6.80	31	2.7
MAS	9.48	0.286	9.00	9.80	12	3.0	9.42	0.223	9.00	9.90	31	2.4
BTB	1.81	0.090	1.64	1.97	10	5.0	1.84	0.135	1.56	2.13	28	7.3
BUL	4.06	0.116	3.94	4.26	11	2.9	4.02	0.109	3.77	4.20	28	2.7
BAS	6.20	0.174	5.82	6.48	10	2.8	6.23	0.208	5.82	6.60	24	3.3
M^3L	0.81	0.057	0.74	0.90	7	7.0	0.81	0.047	0.74	0.90	20	5.7
M^3B	2.10	0.145	1.80	2.26	7	6.9	2.07	0.090	1.93	2.26	19	4.3
PAL	6.65	0.191	6.50	6.90	4	2.9	6.56	0.229	6.10	7.00	23	3.5

N. daedalus

	Female						Male					
	Mean	s.d.	Min	Max	N	CV	Mean	s.d.	Min	Max	N	CV
EAR	23.52	1.355	20.5	25.1	13	5.8	23.75	1.083	21.9	25.8	17	4.6
D1	6.61	0.500	6.0	7.7	12	7.6	6.34	0.280	6.0	6.8	10	4.4
FA	43.30	1.597	40.2	45.8	13	3.7	40.52	1.561	38.3	43.7	18	3.9
D31	41.39	1.720	38.3	43.4	13	4.2	38.61	1.630	36.8	42.6	18	4.2
D32	16.08	0.728	15.1	17.3	12	4.5	15.20	0.503	14.5	15.8	10	3.3
D33	14.30	0.858	13.0	16.2	12	6.0	13.67	0.397	12.9	14.1	10	2.9
D51	40.93	1.213	38.9	42.8	13	3.0	38.73	1.087	37.3	41.8	18	2.8
D52	10.93	0.602	9.8	11.7	12	5.5	10.30	0.488	9.5	11.1	10	4.7
D53	9.57	0.631	8.7	10.8	12	6.6	8.74	0.690	7.7	9.7	10	7.9
HL	20.74	0.906	19.6	22.0	11	4.4	19.37	0.798	18.2	21.5	17	4.1
WT	12.07	1.629	10.2	13.2	3	13.5	7.88	0.954	6.5	9.0	10	12.1
CON	16.12	0.342	15.60	16.60	9	2.1	15.55	0.262	15.20	16.10	15	1.7
GL	17.68	0.465	17.00	18.30	8	2.6	17.09	0.318	16.72	17.70	15	1.9
CM^3	6.60	0.200	6.30	6.90	9	3.0	6.30	0.184	5.90	6.60	15	2.9
C^1-C^1	5.17	0.218	4.90	5.50	9	4.2	4.96	0.145	4.70	5.20	15	2.9
ZYG	11.23	0.466	10.50	11.90	9	4.2	10.72	0.353	10.20	11.30	15	3.3
INT	3.69	0.169	3.40	4.00	9	4.6	3.59	0.108	3.50	3.90	15	3.0
M^3–M^3	7.24	0.235	6.90	7.50	9	3.2	6.98	0.191	6.60	7.30	15	2.7
BRH	6.46	0.260	6.10	6.90	9	4.0	6.30	0.191	6.00	6.60	15	3.0
MAS	9.40	0.387	8.80	9.90	9	4.1	9.11	0.283	8.80	9.70	15	3.1
BTB	2.14	0.215	1.80	2.46	9	10.0	2.02	0.170	1.72	2.38	15	8.4
BUL	3.71	0.085	3.53	3.77	8	2.3	3.69	0.128	3.44	3.85	15	3.5
BAS	5.92	0.249	5.58	6.31	9	4.2	5.74	0.248	5.41	6.30	13	4.3
M^3L	0.82	0.054	0.74	0.86	9	6.6	0.78	0.054	0.70	0.86	9	7.0
M^3B	2.05	0.100	1.85	2.21	9	4.9	1.96	0.074	1.88	2.13	9	3.8
PAL	6.47	0.197	6.20	6.80	6	3.0	6.24	0.217	5.90	6.65	13	3.5

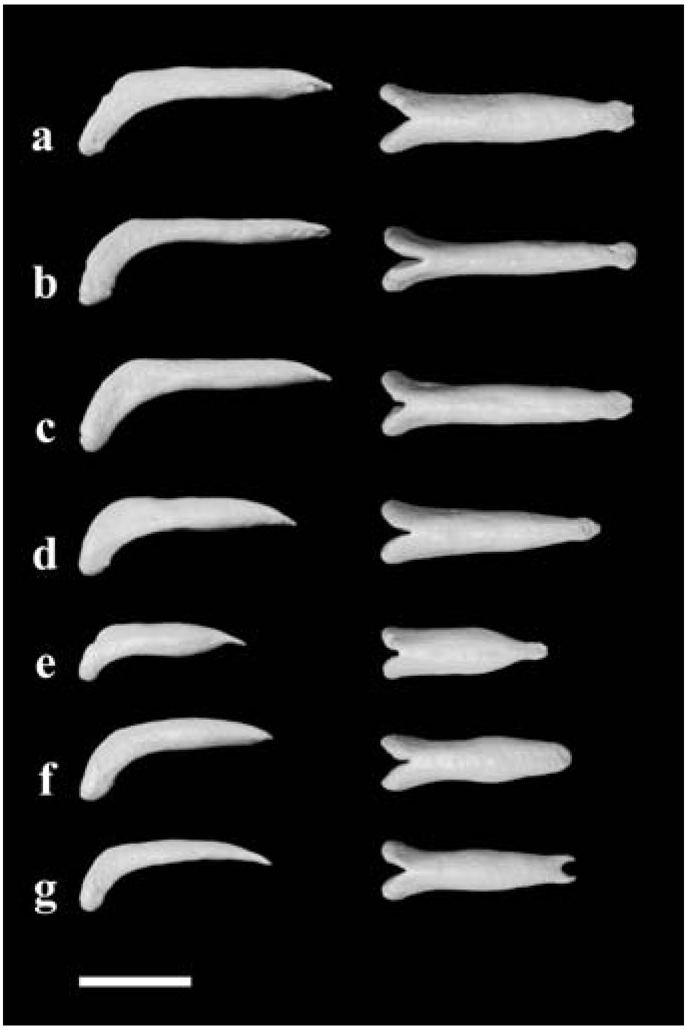


Figure 5. X-ray CT scans of the baculum showing lateral (left), and dorsal (right) views of: **a)** *N. major major* (AM39797); **b)**, *N. m. tor* **subsp. nov.** (WAM63601); **c)** *N. corbeni* **sp. nov.** (AM38833); **d)**, *N. sherrini* (AM34455); **e)**, *N. gouldi* (AM38841); **f)**, *N. daedalus* (AM34451); and **g)**, *N. bifax* (CM11628). Scale bar represents 2 mm.

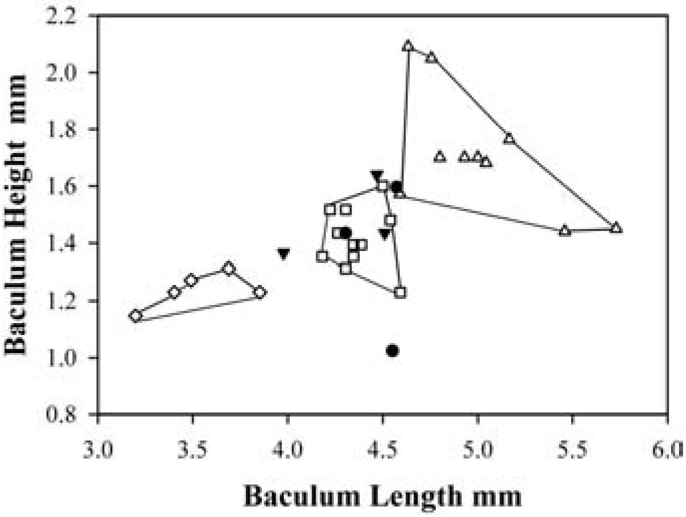


Figure 6. Plot of Baculum Height vs Baculum Length for *N. corbeni* **sp. nov.** (△), *N. major major* (●), *N. m. tor* **subsp. nov.** (□), *N. sherrini* (▼) and *N. daedalus* (◊).

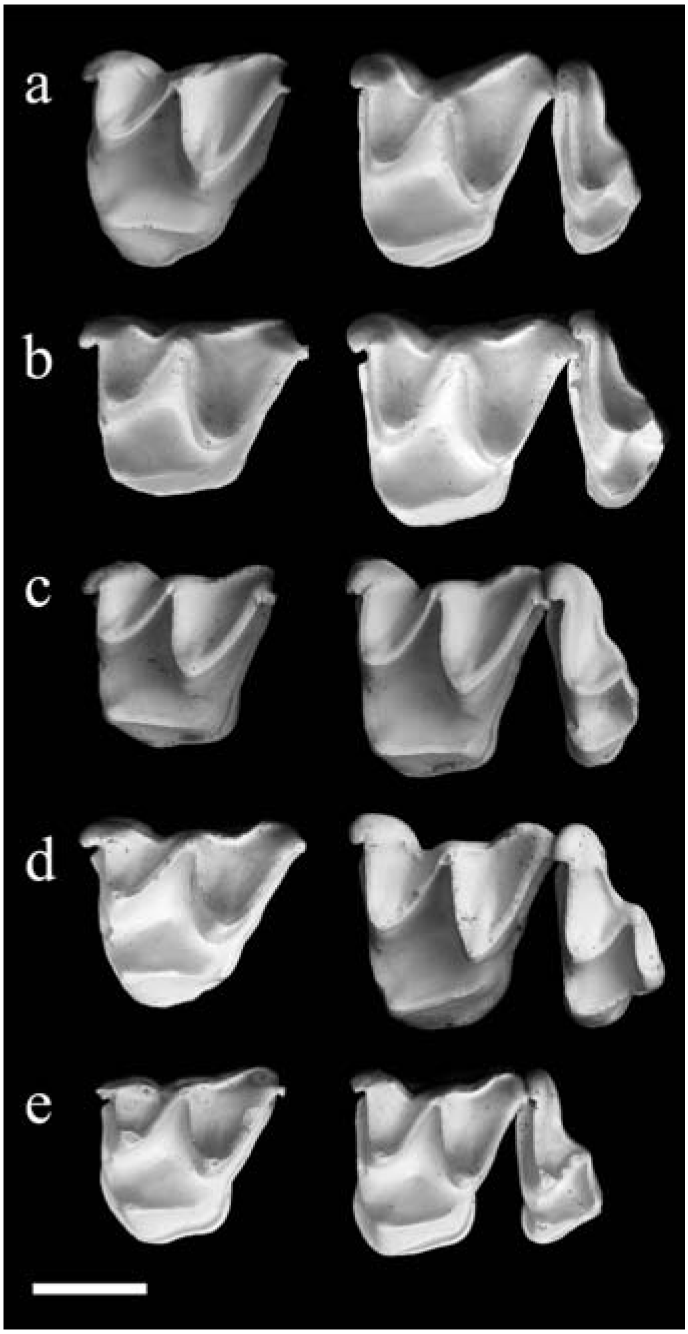


Figure 7. Scanning electron micrographs of left M^1 (left), M^2 and M^3 (right) of: **a)**, *N. corbeni* **sp. nov.** (AM3909, female); **b)**, *N. major major* (AM6319, male) **c)**, *N. m. tor* **subsp. nov.** (AM35884, male); **d)**, *N. sherrini* (AM37936, male) and **e)**, *N. gouldi* (AM3912, male). Scale bar represents 1 mm.

distal median dorsal serrated ridge; distal tip of baculum not fully ossified, occasionally with very weak notch compared to solid point; baculum length > 4.6 mm vs 2.4 - 2.9 mm (n = 13 for mainland and Tasmanian *N. geoffroyi*).

Etymology: Named in honour of Christopher John Corben, bat researcher, frog expert, ornithologist and technophile, in recognition of his contribution to Australian zoology from his largely unfunded pioneering development and ceaseless refinement of technology and software for detection, storage and analysis of bat echolocation calls which has revolutionised bat research and inventory in Australia and on other continents.

Distribution: Drier areas of Queensland, New South Wales and South Australia (see Fig. 8). Most records are from inland of the Great Dividing Range. The most northerly record is from Yebna Station, 80 km west of Taroom, Queensland; Danggali Conservation Park, South Australia is the most westerly locality for which I have examined specimens; however, specimens from Canegrass, South Australia (33° 35' 37" S, 140° 03' 06"E; SAM 17320-21) identified from gene sequencing (B. Appleton, T. Reardon, *et. al.* in progress) represents the most western record of the species. The western distribution of this species appears to be truncated by the Flinders Ranges in South Australia. A comprehensive review of field records of this species is presented by Turbill and Ellis (2006).

This species is sympatric with *N. geoffroyi* throughout its entire range; in the southern and eastern parts of its range it shows extensive sympatry with *N. gouldi*.

Specimens examined: A total of 64, see Appendix.

Remarks: The presence of this large distinctive species in eastern Australia was evidently overlooked until Hall and Richards (1979) drew attention to its distinction from *N. gouldi* and summarised distribution data for the few specimens available (as *N. timoriensis*).

Larger examples of *N. gouldi* from higher rainfall areas are of the same general size as *N. corbeni* **sp. nov.** In particular, FA measurements (used extensively in field identifications of *Nyctophilus*) show broad overlap between each species for each sex. However, *N. corbeni* **sp. nov.** has a noticeably broader head and snout, as reflected by C^1-C^1: for males, *N. gouldi* maximum = 5.2 mm (n=85) vs minimum for *N. corbeni* = 5.7 (n=26); for females, maximum for *N. gouldi* = 5.4 (n=58) compared with minimum of 5.9 (n=15) for *N. corbeni*. The two species are broadly sympatric inland of the Great Dividing Range in northern and northwestern Victoria, New South Wales and Queensland and both species have been captured in the same trap on the same night. Inland *N. gouldi* are generally smaller than those of montane or subcoastal regions (Parnaby 1987; Lumsden 1994; Young and Ford 2000) and are readily distinguished from *N. corbeni* **sp. nov.**, as seen in a plot of FA vs C^1-C^1 (Fig. 9).

Nyctophilus major Gray, 1844

Holotype: NHM no. 44.7.9.20, male skin and skull. Collected by J. Gilbert 20 March 1843 (Mahoney and Walton 1988). Gilbert's field number 23 (J. Mahoney *pers. comm.* 1984).

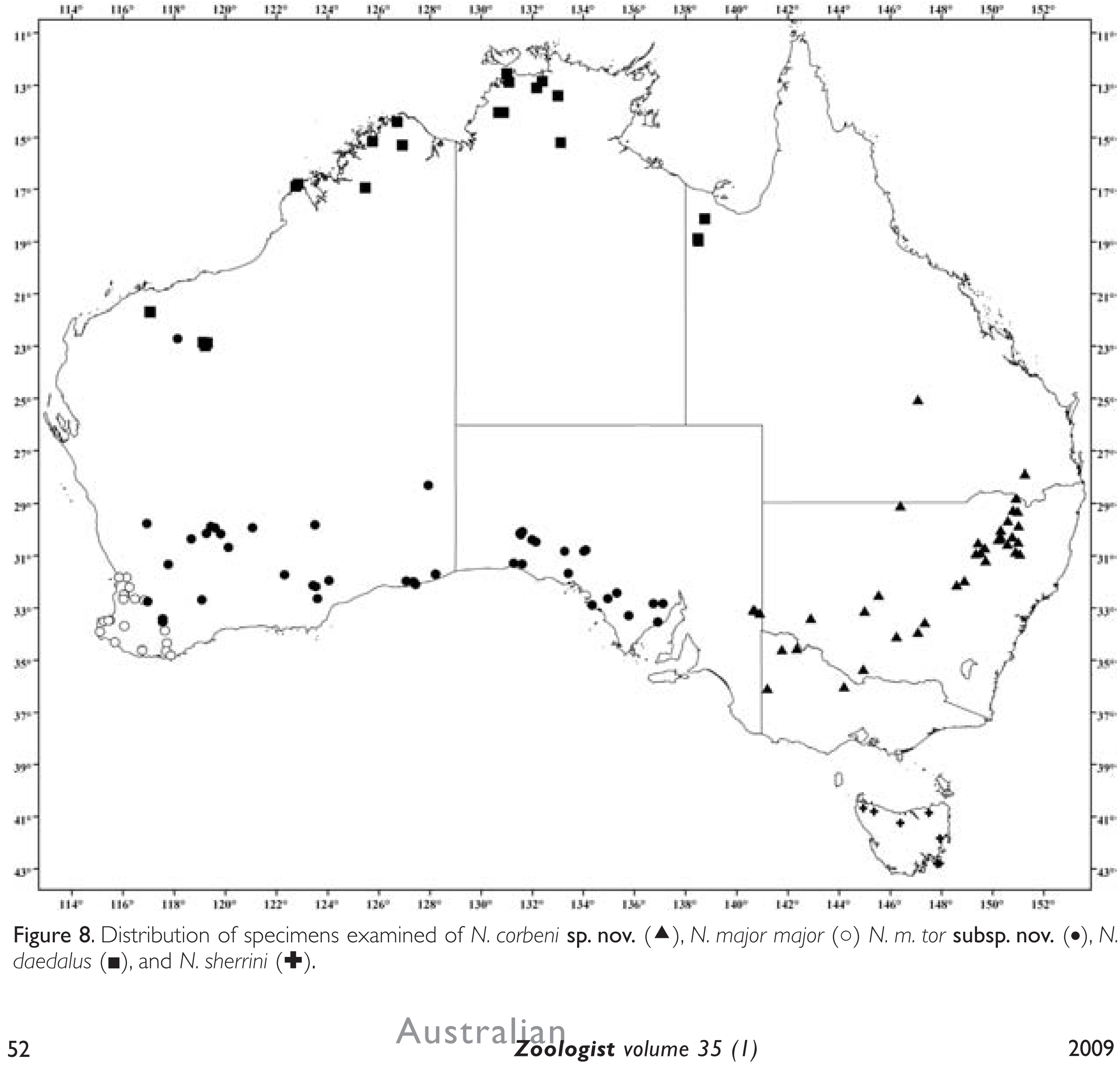


Figure 8. Distribution of specimens examined of *N. corbeni* **sp. nov.** (▲), *N. major major* (○) *N. m. tor* **subsp. nov.** (●), *N. daedalus* (■), and *N. sherrini* (✚).

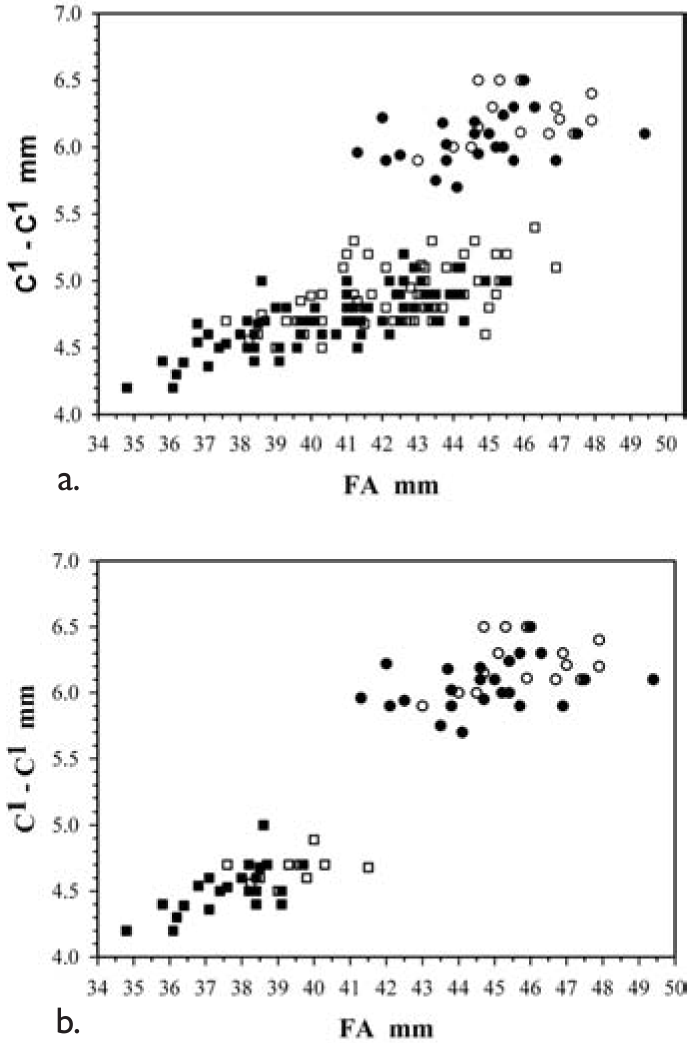


Figure 9. Plot of C^1–C^1 vs FA showing separation of adult *N. gouldi* (□) and *N. corbeni* **sp. nov.** (○), sold symbols are males. **a)**, *N. gouldi* from all localities in southeastern Australia; **b)**, *N. gouldi* from inland of the Great Dividing Range from Victoria to Queensland.

Type locality: Perth, Western Australia.

Re-diagnosis (of nominotypical form): *Nyctophilus major major* differs from *N. corbeni* **sp. nov.** in: its relatively narrower skull (Figs 3 and 10; Table 4); relatively narrower and less rounded zygomatic arches; narrower braincase; squarer more nearly parallel-sided rostrum; proportionally longer palate (Fig. 4); usually smaller, more slender baculum; relatively more reduced protocone on M^1 resulting in more truncated lingual margin (Fig. 7).

It differs from *N. gouldi* in: its more reduced third molars; baculum longer, > 4.0 mm with more slender shaft. It is further distinguished from southwestern Australian populations of *N. gouldi* in: its considerably larger size; more massive, narrower skull; larger rostrum; conspicuously more reduced protocone on M^1 and larger, more slender baculum.

It differs from *N. sherrini* in: its relatively broader, more massive skull; relatively broader rostrum, C^1–C^1 > 5.6 mm; relatively smaller bullae; relatively more reduced protocone on M^1 and M^2 resulting in a more truncated lingual margin (Fig. 7); reduced third molars with metacone absent and third commissure obsolete rather than well developed; relatively narrower INT; and relatively shorter proximal end on the baculum.

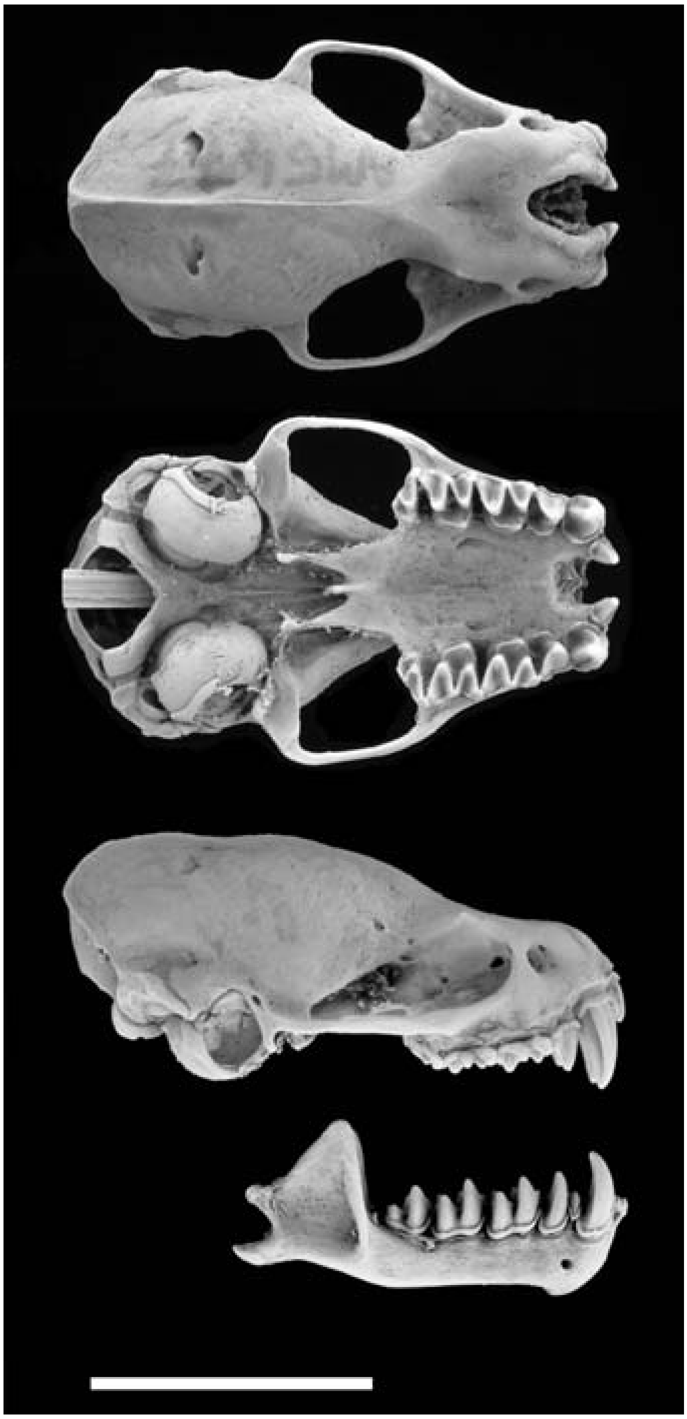


Figure 10. Photographs of the skull and dentary of a young adult male *N. major major* (AM5477) from Tambellup, Western Australia. Scale bar represents 10 mm.

It differs from *N. daedalus* in: its larger skull size (Table 4); larger bullae; darker fur colour; larger baculum, baculum length > 4.0 mm (Table 3, Figs 5 and 6) with a more slender shaft.

Skull readily distinguished from that of *N. howensis* by conspicuously smaller skull dimensions, more reduced M^3 (see also re-diagnosis of that species).

Distribution: Southern Australia from the southwest corner, east to Eyre Peninsula of South Australia (Figs. 8 & 11). Two subspecies are distinguished (see below), the nominotypical form in southwestern Western Australia, and a new subspecies from the wheatbelt of Western Australia, east to Eyre Peninsula.

Material examined: A total of 43 specimens of the nominotypical form, listed in the Appendix. Six specimens are referred to an inland subspecies, described below. Black and white photographs of the holotype skull and dentary of *N. major major*.

Remarks: Nominotypical *N. major* and *N. corbeni* **sp. nov.** are morphologically very close, with considerable overlap in both external and craniodental metric variation. They are distinguished by proportional differences in the cranium, as noted above, and by the development of the protocone on M^1**,** which is usually larger in *N. corbeni* **sp. nov.,** resulting in a more rounded lingual margin (Fig. 7). On external criteria, D3.1 length is usually shorter relative to FA in *N. major major*.

Size variation within N. *major*

Two size morphs are evident within Western Australian samples of *N. major*. Individuals from lower rainfall, typically inland, localities across southern Western Australia are generally smaller in body and skull size than *N. major* from the higher rainfall areas of far south-western Western Australia. Greater variation in body and skull size is evident amongst specimens from districts of intermediate rainfall, viz. the Dryandra woodlands of the wheatbelt, as well as the subcoastal districts of elevated rainfall around Balladonia and the Roe Plain. The majority of specimens examined from these districts are relatively small but there are a small number of animals that are as large as those from high rainfall districts, as well as some animals of intermediate size. The following assessment of size variation in *N. major* focuses on specimens from Western Australian localities.

The variation within *N. major* is evident in a plot of ZYG against GL for females (Fig. 12a). In the wheatbelt region, two adult females from the Katanning district fall into each of the large and small morphs, as do the two females from the Woodanilling area, 18 km northwest of Katanning. In the Roe Plains area south of the Nullarbor Plain in eastern Western Australia, one of two females from different localities south of Madura falls within the small morph and the other is intermediate but closest to the small morph, while a female from Kuthala Pass on the edge of the Hampton Tableland at Mundrabilla, clearly falls within the large morph.

A similar, though less clear, trend is evident in a plot of ZYG against GL for males from all Western Australian localities (Fig. 12b). This includes specimens from the three districts of apparent sympatry between size morphs. The seven animals from Dryandra Woodlands (wheatbelt district) include two that fall within the small morph, one that falls within the large morph, and four that are intermediate. Similarly, four animals from the Balladonia district include two that fall within the small morph, one in the large morph, and one intermediate. Five animals from Kuthala Pass,

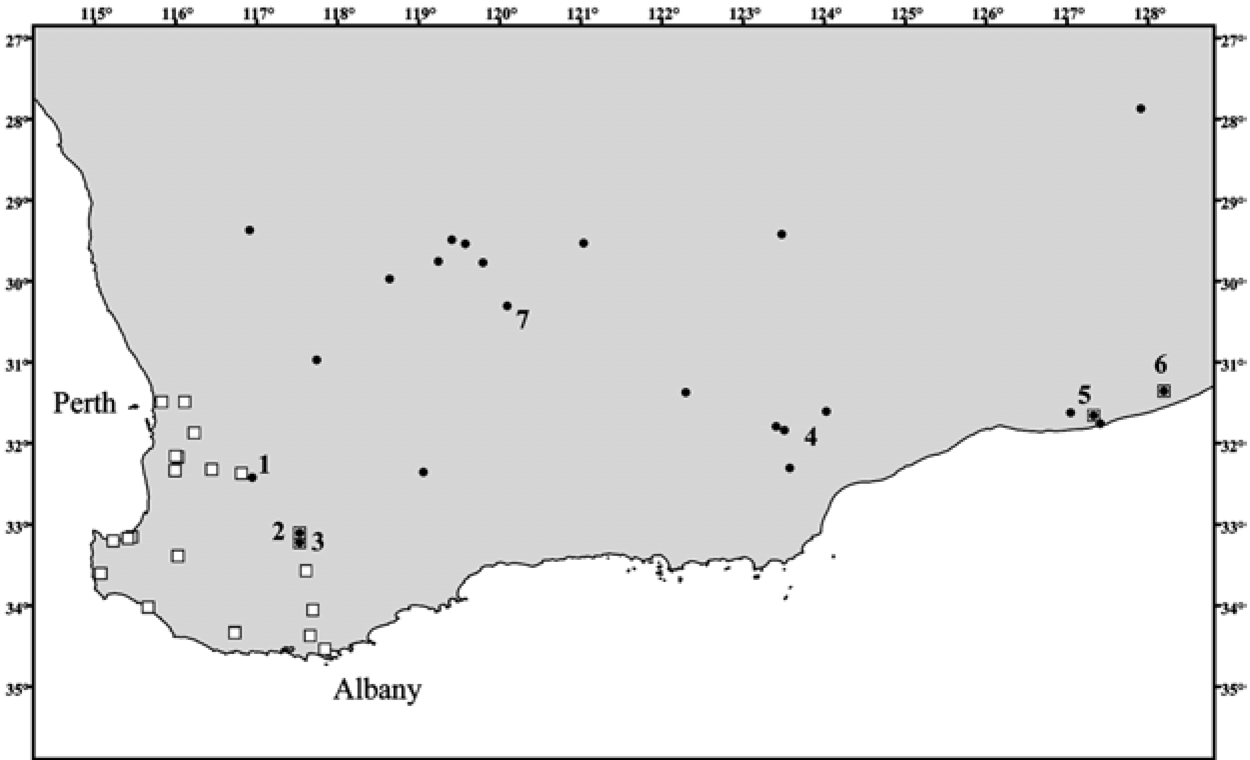


Figure 11. Distribution of *N. major major* (□) and *N. m. tor* **subsp. nov.** (•) based on specimens examined. Districts of near sympatry are: 1, Dryandra woodlands; 2, Woodanilling; 3, Katanning; 4, Balladonia, 5, Madura and Roe Plain, and 6, Kuthala Pass, Mundrabilla – 7, represents the type locality of *N. m. tor* **subsp. nov.**

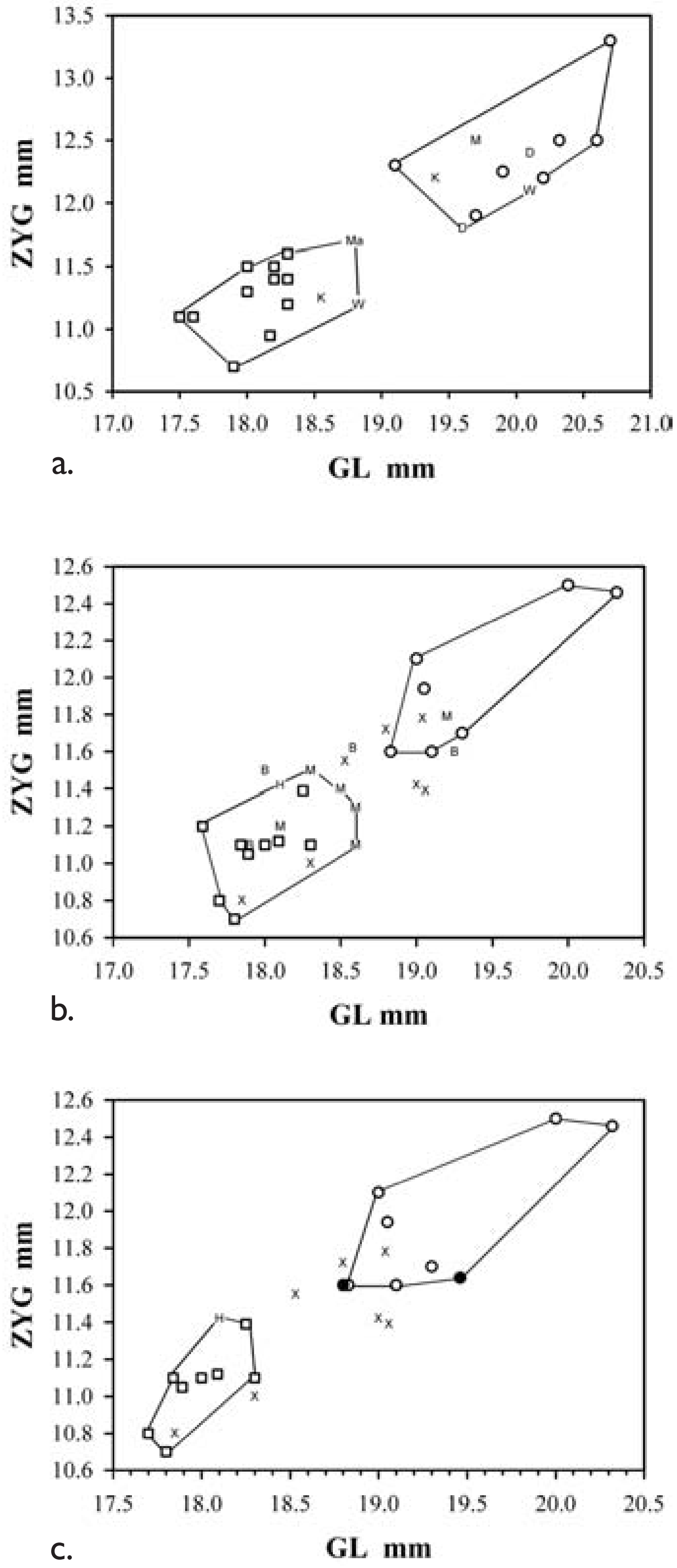


Figure 12. Plot of ZYG vs GL for *N. major major* (○) and *N. major tor* **subsp. nov.** (□). **a)**, adult females from WA and SA; **b)**, males from WA localities; **c)**, males from WA localities west of longitude 122° E. Localities are: B, Balladonia; D, Dwellingup; K, Katanning, M, Mundrabilla; Ma, Madura; W, Wodanilling; X= males from Dryandra Woodlands, wheatbelt, Western Australia. H represents holotype of *N. major tor* **subsp. nov.**

Mundrabilla, on the edge of the Hampton Tableland fall within the small morph, while one from the Madura district of the adjoining Roe Plain, falls within the large morph.

The size contrast between males (few female specimens are available) from inland and the far south-western areas (home of nominotypical *N. major*) is clearest in a plot of ZYG against GL from a more restricted region, localities west of longitude 122°E in Western Australia (Fig. 12c). Of the seven males from Dryandra woodlands, two fall within the smaller inland morph, two fall within or close to the large morph, and the remaining three could be considered to be intermediate.

The small magnitude of the differences that separate the two morphs on the basis of individual measurements (often less than 1 mm) is deceptive. For example, measurements for two adult females representing both morphs from the Katanning district are respectively, GL 19.4 mm vs 18.5 mm, ZYG 12.2 vs 11.2 mm, and MAS 10.0 vs 9.5 mm, yet the size difference is clearly evident from direct comparison of skulls (Fig. 13). This probably reflects the inadequate extent to which standard skull measurements, considered individually, capture overall size and shape differences that are apparent from direct visual comparisons. I know of at least three bat researchers who captured live examples of the small morph and all independently tentatively identified them as *N. gouldi,* i.e. it was recognised as being distinct from larger *N. major*. This indicates that the differences apparent from comparative museum studies are evident in live animals.

Size variation within *N. major* was examined using a Principal Components Analysis (PCA) based on a correlation matrix of FA and nine skull and dental measurements of 67 adult specimens. Measurements were selected for the analysis in order to maximise sample size.

Figure 13. Photographs illustrating differences in skull size between, **left**, *N. major major* (WAM6375); and **right**, *N. m. tor* **subsp. nov.** (AMNH197281): both are adult females from the Katanning district, Western Australia. Scale bar represents 10 mm.

Table 5. Standardised character coefficients and variance for each axis of a PCA based on a correlation matrix of FA and 9 cranial and dental dimensions of *N. major major* and *N. m. tor* **subsp. nov.**.

	PC 1	PC 2
FA	0.847	0.153
CON	0.971	0.102
GL	0.969	0.073
CM^3	0.930	0.085
$C^1–C^1$	0.914	0.072
ZYG	0.929	0.090
INT	0.732	-0.591
M^3-M^3	0.899	0.196
BRH	0.790	-0.426
MAS	0.885	0.072
% variance	79.13	6.34

Standardised coefficients for each measurement on the first PC axis suggest that this axis, which accounts for 79% of the total measurement variance (Table 5), reflects overall skull and FA size because all coefficients are of the same approximate magnitude and sign. Coefficients on the second axis reflect an inverse relationship between INT and BRH, on the one hand, against the remaining measurements. Principal Component scores for specimens on the first two PC axes fall into two broad groups (Fig. 14) which correspond to the two size morphs recognised here. PC scores for most of the 7 specimens (all male) from Dryandra woodlands are intermediate between each group. A partial separation by sex is evident for both morphs on PC 2. A PCA based on the external characters EAR, FA, D31, D51 and HL showed extensive overlap between size morphs and sex (not shown).

Geographic variation in size was examined further by plotting scores for specimens on PC 1, used as an indicator of general size, against longitude (Fig. 15). Three points are evident: a) the greater size of specimens from far south-western Western Australia, including some individuals from the wheatbelt; b), the intermediate size of some individuals from Dryandra; and c) the fact that several individuals from localities south of the Nullarbor Plain fall within the size range for the large size morph, as do two adult males from the Balladonia district.

The integrity of the two size morphs and the relationships of intermediate specimens were examined through a Canonical Variates Analysis (CVA), using the same ten characters and 67 specimens used in the PCA. Specimens were assigned to groups based on size morph and sex, while ten specimens were entered in the analysis ungrouped. The latter series included seven specimens from Dryandra, the large adult male and female from the Mundrabilla region, and a female from the wheatbelt. The first two CV axes captured 98.4% of the variance (Table 6) and a plot of scores for individuals on the first two CV axes (Fig. 16) shows a similar separation of size morphs as on the first axes in the PCA. The jack-knifed classification function assigned all females to the correct size morph, although a substantial proportion was allocated to the wrong sex

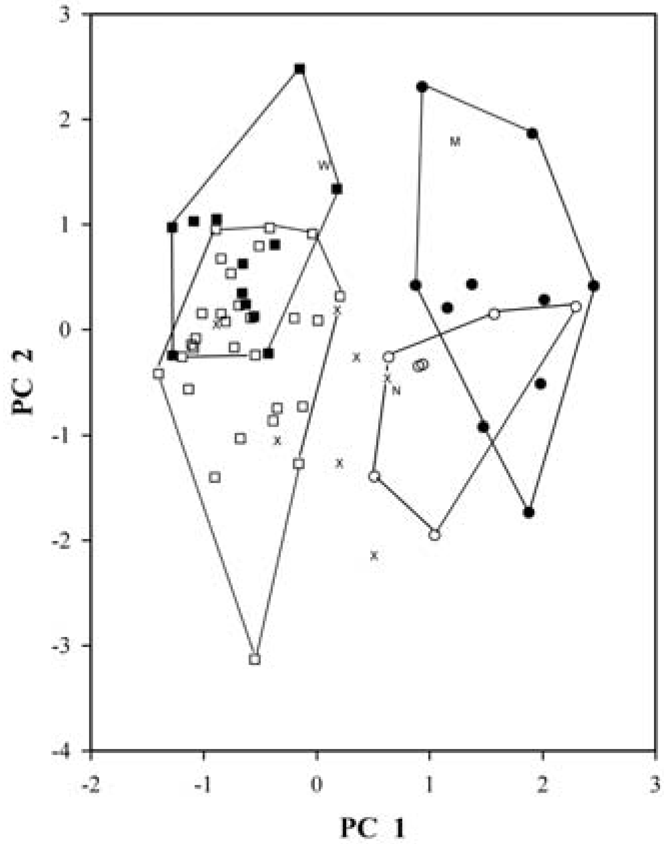


Figure 14. Plot of specimen scores on the first two PC axes for adult *N. major major* (○) and *N. m. tor* **subsp. nov.** (□) based on a PCA of FA and 9 cranial and dental measurements. Females are solid symbols, males are open symbols. Locality designations for ten specimens that were not allocated to a group in the accompanying canonical variates analysis are: seven males from Dryandra (X), a female from Mundrabilla (M), a male from Madura district (N), and a female from Woodanilling (W).

Table 6. Standardised character coefficients, eigenvalues and percentage of total variance for the first three CV axes of a CVA of FA and 9 skull and dental dimensions of *N. major major* and *N. m. tor* **subsp. nov.**

	CV 1	CV 2	CV 3
FA	0.360	0.706	0.089
CON	0.255	-0.010	-1.277
GL	0.293	0.384	1.570
CM^3	0.173	-0.886	0.819
$C^1–C^1$	-0.044	-0.519	-0.194
ZYG	0.016	0.367	-0.071
INT	0.237	-0.166	-0.454
M^3-M^3	0.206	0.943	-0.701
BRH	0.185	-0.597	-0.230
MAS	-0.255	-0.404	0.012
Eigenvalues	5.386	0.710	0.096
% variance	87.0	11.4	1.6

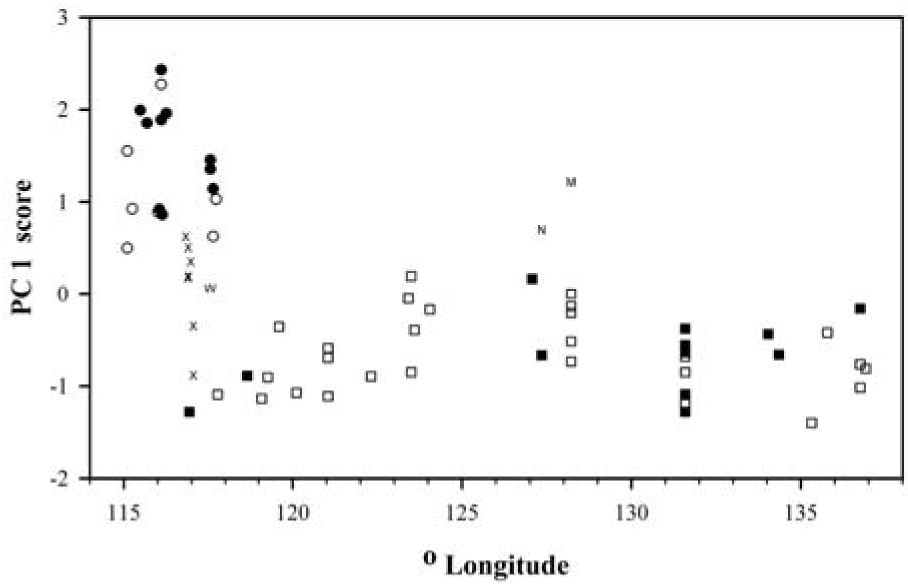


Figure 15. Plot of PC 1 scores vs longitude for adult *N. major major* (○) and *N. m. tor* **subsp. nov.** (□) from a PC analysis using FA and 9 cranial and dental measurements. Solid symbols represent females, open symbols are males. The ten specimens entered in the CVA as ungrouped are indicated as per the caption for Fig. 14.

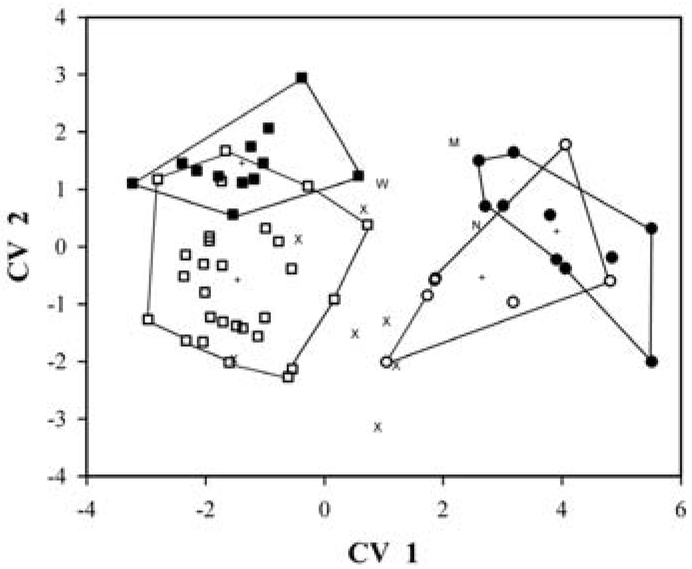


Figure 16. Plot of specimen scores on first two CV axes for adult *N. major major* (○) and *N. m. tor* **subsp. nov.** (□) based on an analysis using FA and 9 skull and dental characters. Females Solid symbols represent females, open symbols represent males; (+) indicates the group centroid for each sex. The ten specimens entered in the CVA as ungrouped are indicated as per the caption for Fig. 14.

(Table 7). Of the 10 specimens not allocated to a group prior to the analysis, 3 of the 7 male Dryandra specimens were allocated to males of the small morph, 3 to males of the large morph and 1 to the female small morph. The remaining three specimens were allocated to the respective sex and morph expected on the basis of size, viz. the female from Kuthala Pass and the male from Madura to the large morph, the small female from Woodanilling to the small morph. (Several key female specimens from the wheatbelt were excluded from the CVA due to missing measurements). The intermediate nature of these specimens is confirmed by the PCA and CVA. However, the classification of intermediate specimens in the CVA should be interpreted with caution due the small sample sizes. Further, CVA performs poorly when allocating specimens that form a gradation compared with discrete groups because it maximises between-group differences relative to within-group variation.

Three scenarios can be invoked to explain size variation within *N. major*, none of which were unequivocally rejected by this study. The simplest is that size variation is a response to environmental factors, such as moisture or temperature gradients. It is not surprising that animals from lower rainfall areas are, on average, smaller. Alternatively, two or more crypticspecies might exist in the region,

Table 7. Results of jackknife classification function of CVA of FA and 9 skull and dental dimensions of *N. major major* and *N. m. tor* **subsp. nov.**, showing number of misclassified specimens per group, and allocation of 10 specimens entered in the CVA as ungrouped.

	Female *N. m. tor* subsp. nov.	Female *N. m. major*	Male *N. m. tor* subsp. nov.	Male *N. m. major*	% correct
Female	9	0	3	0	75
Female *N. m. major*	0	5	0	5	50
Male *N. m. tor* subsp. nov.	5	0	22	1	79
Male *N. m. major*	0	3	1	3	43
Total	14	8	26	9	68
Ungrouped *a priori*	2	1	3	4	

either with complete reproductive isolation but a degree of morphometric overlap, or with hybridisation and/or introgression. If the latter scenario is correct, the likely zone of interaction is in the wheatbelt region of south-western Western Australia, and at locations of elevated rainfall along the southern, near coastal areas of eastern Western Australia. Irrespective of the significance of the size morphs, it is clear that they co-occur; in at least one instance, both were captured on the same night at the same site. An adult lactating female from Kuthala Pass, near Mundrabilla Hotel (WAM22953) falls within the large morph (e.g. Fig. 12a) and groups with the large morph in the PCA (Fig. 14) and CVA (Fig. 16). Eight adult males of the small morph were evidently captured in the same trap with this specimen. The other instances of apparent sympatry or parapatry between size morphs occur in several districts, as noted previously. However, sympatry or close parapatry, perhaps due to habitat separation, cannot be established due to imprecise locality data. This is problematic, given that steep gradients in rainfall and vegetation changes occur over comparatively short distances in these areas.

On balance, I suspect that two cryptic species are present, which are broadly sympatric in the wheatbelt and in southern subcoastal areas of eastern Western Australia. However, although the data are suggestive of two species, I am unable to refute the simpler hypothesis of a variable species with environmentally induced size variation, for which infra-specific variation is inadequately defined in this study due to the limited number of specimens available from strategic locations. Resolution of this complex problem will depend on further, targeted collecting and detailed genetic investigations using multiple markers to document the contemporary pattern of gene flow between populations. In the interim, one option is to treat *N. major* as a single, highly variable taxon. Another is to recognise the small size morph as a distinct taxon, but at subspecific level within *N. major*. While this action might be unpopular at a time when the subspecies category is treated by many taxonomists as an essentially meaningless entity, it is taken in this instance for several reasons: 1) it enables a refinement in diagnoses and identification of other southern Australian *Nyctophilus*; 2) formal recognition of the small morph will reduce the risk of future confusion with *N. gouldi*; and 3) providing the small morph of *N. major* with a formal identity should lead to greater likelihood that it will attract the further work that is needed to determine its true status.

Nyctophilus major tor subsp. nov.

Holotype: WAM63601 (previously AM39782), field number 7HP51, adult male body fixed in 80% ethanol and stored in 75% ethanol, skull extracted and cleaned. Penis stored separately in 75% ethanol. Liver sample stored in 95% ethanol (field number 48159) held at the Australian Museum and liver sample (field number 48120) stored in liquid nitrogen held at the South Australian Museum. Captured in a bat trap (harp trap) set next to Johnnies Dam by T. Reardon, A. Reside, A. Scanlon and H. Parnaby, 2 December, 2007. Dimensions of the holotype are given in Table 2.

Paratypes: A total of five, field number in brackets: AM M39815 (7HP50) adult male, skull extracted, body fixed in 80% ethanol and stored in 75% ethanol, captured in a mist net by T. Reardon, A. Reside, A. Scanlon and H. Parnaby, 2 December, 2007 at Johnnies Dam, Jaurdi Station, 30° 46'S 120° 07' E. Liver sample stored in 95% ethanol and held at the Australian Museum, liver sample stored in liquid nitrogen held at the South Australian Museum; AM M39801 (7HP46), adult female body fixed in 80% ethanol and stored in 75% ethanol, skull extracted, captured in a mist net by T. Reardon, A. Reside, A. Scanlon and H. Parnaby, 29 November, 2007 at Eagle Rock, approximately 105 km NW of Southern Cross, Goldfields district, WA 30° 26' 17"S, 118° 40' 31"E. Liver sample (field number 48170) stored in 95% ethanol held at the Australian Museum, liver sample stored in liquid nitrogen stored at the South Australian Museum; AM38843 (WA08), adult male with skull extracted, AM38844 (WA09), adult male with skull extracted, and AM38845 (WA10) adult male, with skull extracted - bodies of all three were fixed in 10% formalin and stored in 75% ethanol and all three captured in mist nets by M. Pennay, T. Reardon, A. Reside, and A. Scanlon, 13 November, 2007, Goongarrie Station, WA, 29° 59.528'S, 121° 03.464' E. Liver samples of the latter three specimens are stored in liquid nitrogen held at the South Australian Museum.

Type locality: Johnnies Dam, Jaurdi Station, 30° 46' 22"S, 120° 07' 55"E, 125 km west of Kalgoorlie, Western Australia. Altitude approximately 435 m.

Diagnosis: It differs from nominotypical *N. major* in: smaller average size, e.g. FA for adult females typically < 44 mm, adult males typically <42 mm; GL < 18.8 mm; CM^3 mostly < 7.1 mm; $C^1–C^1$ usually < 5.7 mm; relatively longer ears, and in relatively longer baculum (Fig. 6). Means of all external, skull and dental dimensions are smaller, see Table 4. The protocone of M^1 and M^2 is often more reduced in *N. m. tor* **subsp. nov.**, resulting in a more truncated lingual margin (Fig. 7) and M^3 is often slightly more reduced.

It differs from *N. corbeni* **sp. nov.** in: its smaller overall body and skull size; e.g. adult male mean FA 40.94 mm vs 44.72 mm, mean GL 18.04 mm vs 19.20 mm; skull relatively narrower and conspicuously less robust (Fig. 3 and Fig. 17, Fig. 18): ZYG < 11.7 mm vs > 12.2 mm (females), < 11.6 mm vs > 11.9 mm (males); PAL relatively longer (Fig. 4, Table 4); mean baculum length shorter, 4.38 mm vs 4.97 mm and ≤ 4.6 mm, with proportionately broader base: mean Baculum Breadth 1.18 mm vs 1.24 mm.

It differs from *N. sherrini* in: smaller size; skull relatively broader, with broader zygomatic arches and broader rostrum; PAL relatively shorter (Fig. 4); INT relatively narrower; third molars far more reduced: third commissure of M^3 rudimentary and metacone absent (Fig. 7); protocone on M^1 and M^2 more reduced resulting in far more truncated lingual margin (Fig. 7); baculum of equivalent length but with more slender main shaft.

It differs from *N. daedalus* in: its darker fur colour; generally larger size; longer baculum (> 4.0 mm), narrower skull; relatively larger bullae, narrower mesopterygoid fossa; basisphenoid pits shallow or absent; less reduced third molars.

Figure 17. X-ray CT scans of the holotype skull of *N. major tor* **subsp. nov.**, WAM63601 adult male. Scale bar represents 10 mm.

It differs from *N. bifax* in: grey-brown dorsal fur colour rather than tawny brown: postnasal elevation relatively higher rather than a low rounded bump; proportionately larger skull, GL larger for equivalent FA; relatively larger bullae; third molars far more reduced, third commissure of M^3 rudimentary rather than being subequal to second commissure (Fig. 7 and Fig. 21); distal tip of baculum a simple point or with a weak notch compared to strong distal bifurcation, baculum length > 4.1 mm vs < 3.9 mm; glans penis with relatively much larger urethral lappets, and in which the distal tip is a simple rounded point, rather than being enlarged into a sub-spherical protrusion as in *N. bifax*.

It differs from eastern Australian *N. gouldi* in: relatively more reduced protocone on M^1 and M^2 resulting in more truncated lingual margin (Fig. 7); more reduced third molars, metacone absent; generally more robust skull; and a larger more slender baculum shaft; baculum length > 3.8 mm. Although few specimens of *N. gouldi* were available from south-western Western Australia, this population is distinguished from *N. m. tor* in: its smaller overall size; less massive skull; relatively larger bullae; unreduced third molars in which the metacone is well

Figure 18. Photographs of the skulls of *N. corbeni* **sp. nov.** (C3240; left) and *N. m. tor* **subsp. nov.** (WAM22973; right) showing relatively broader and more robust skull of *N. corbeni*. Both are adult males. Scale bar represents 10 mm.

developed. Although ranges of FA for equivalent sex for adults overlap between both taxa, *N. gouldi* is clearly a smaller animal, as reflected by C^1–C^1: adult females mean = 4.72 mm (4.6–4.8, n = 4) compared with mean = 5.43, > 5.0; adult males mean = 4.46 mm (4.3–4.63, n = 5) compared to mean = 5.38, > 5.0 mm.

It differs from *N. nebulosus* in: relatively narrower INT; relatively longer CM^3; bullae relatively smaller and set further apart; more reduced third molars: greater reduction of third commissure of M^3 and metacone absent; baculum with relatively more slender shaft and longer, > 4.1 mm vs < 3.0 mm.

It differs from *N. heran* in having far less developed post-nasal elevation, which is a rounded mound consisting of a pair of mounds separated medially by a thin vertical groove compared with paired mounds joined medially by a conspicuous membrane that expands distally to form a "Y" shape; C^1–C^1 > 5.0 mm vs 4.5 mm; main shaft of baculum thicker.

It differs from *N. geoffroyi* in: having a simpler post-nasal elevation which has a simple median vertical grove, rather than an more developed pair of mounds joining in the distal mid-line by an elastic membrane which forms a distinctive "Y"-shaped structure; by larger average size, e.g. compared to South Australian and southern Western Australian *N. geoffroyi*, adult female mean FA 41.34 mm vs 36.32 mm (33.6–39.6, n = 48), males 40.94 mm vs 34.87 mm (32.3–37.7, n = 28); having GL > 16.7 mm; C^1–C^1 > 4.8 mm, CM^3 > 6.1 mm; relatively smaller bullae; more reduced M^1 protocone such that lingual margin is truncated rather than convex; M^3 more reduced with more rudimentary third commissure and metacone not present; baculum > 3.8 mm; and distal tip of glans penis blunt and rounded rather than forming an elongate "beak", lacking a distal median dorsal serated ridge; distal tip of baculum not fully ossified, with very weak notch compared to solid point; baculum length > 4.1 mm vs < 2.9 mm (n = 13 for mainland and Tasmanian *N. geoffroyi*).

Skull readily distinguished from *N. howensis* by conspicuously smaller skull dimensions, more reduced M^3 which lacks a metacone, and as indicated in the re-diagnosis of that species.

Etymology: a random combination of letters, selected for brevity.

Distribution: Throughout Western Australia south of the Hamersley Range and across South Australia as far east as the Eyre Peninsula (Fig. 8). It appears to be absent from far south-western Western Australia. In addition to extensive sympatry with *N. geoffroyi*, this species is closely parapatric with *N. daedalus* in the Hamersley Range of north-western Western Australia.

Specimens examined: A total of 92, see Appendix.

Remarks: Formal recognition of the smaller morph as a subspecies of *N. major* represents a further step toward clarification of the taxonomy of this group but it is a compromise, pending a more detailed assessment using an integrated morphometric and genetic approach. The relatively small sample available for *N. major major* has hindered an assessment of individual variation in that taxon. Field workers in Western Australia should be alert to the possibility that the small morph could occur in the higher rainfall areas of the far south-west.

The type locality of *N. major* is given as "Perth" (Thomas 1915) and Mahoney and Walton (1988) note that the collection date on the holotype label is three days after the collector, Gilbert, returned to Fremantle from the Houtman Abrolhos. Whittell (1942) notes that little is known of the collecting itinerary during the time Gilbert left Perth on a trip overland to Albany, but that the route went via the settlements of Williams (30 km south-west of Narrogin) and Kojonup. It is therefore possible that the holotype of *major* was collected during the overland trip, within the geographic range of *N. m. tor* **subsp. nov.**, as both taxa occur on the western edge of the wheatbelt. I have examined high quality photographs of the holotype skull of *N. major* but have not had the opportunity to examine the holotype. The available dimensions of the holotype of *N. major* (Table 2) exceed the maximum recorded dimensions of *N. m. tor* **subsp. nov.** for a number of characters: ZYG of 12 mm exceeds the upper range of 11.6 mm, although the zygomatic arches are broken on one side, measurements taken from the scaled photograph suggest that it was at least 12 mm; CM^3 of 7.3 mm exceeds the upper range of 7.1 mm for *N. m. tor* **subsp. nov**. Other available measurements of the holotype of *N. major* fall within the overlap of ranges of males between each taxon for FA, M^3-M^3 and INT. GL as given in Table 2 falls within the range for *N. m. tor* **subsp. nov**; however, this measurement is incomplete because the posterior of the braincase is missing in the holotype (Fig. 2). The holotype groups within the nominotypical *N. major* cluster in a plot of FA vs CM^3 (Fig. 19) and also in a plot of FA vs ZYG (not shown). Consequently, the holotype of *N. major* is unlikely to be an example of the small morph, herein designated as *N. major tor* **subsp. nov**.

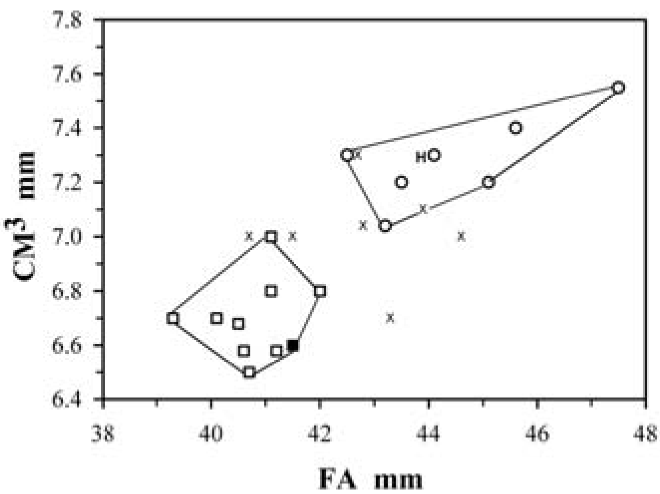


Figure 19. Plot of CM^3 vs FA for adult male *N. major major* (○) and *N. m. tor* **subsp. nov.** (□) from localities west of longitude 122°E, showing the size of the holotype skull of *N. major* (H) relative to seven adult males from Dryandra Woodlands (X) and the holotype of *N. m. tor* **subsp. nov.** (■).

Nyctophilus daedalus Thomas, 1915

Holotype: NHM No. 97.4.12.8, adult male in alcohol collected by Knut Dahl.

Type Locality: Daly River, Northern Territory.

Re-diagnosis: A moderate to large species, closely resembling *N. major tor* **subsp. nov.** but differing in: paler fur colour; generally smaller; relatively broader skull; moderate to deep basisphenoid pits; baculum length < 4.0 mm with a relatively larger proximal end (Fig. 5); and smaller bullae which are relatively further apart, as indicated by a plot of BTB against CON (Fig. 20).

It differs from *N. bifax* in: having a relatively broader skull; relatively smaller and more reduced third molars (Fig. 21); the presence of a slight notch on the distal tip of the baculum which is never deeply bifurcate as in *N. bifax*; and a pronounced difference in the external morphology of the glans penis which has relatively much larger urethral lappets and lacks the large rounded distal protuberance present in *N. bifax* (Fig. 22).

It differs from *N. gouldi* in: generally relatively smaller postnasal prominence; a generally broader and more robust skull; more reduced protocone on M^1 and M^2 resulting in truncated rather than strongly convex lingual margin; far more reduced third molars, metacone absent and third commissure obsolescent rather than subequal to second commissure; bullae that average smaller and are set further apart: the bullae are closer together in *N. gouldi* of equivalent BUL (Fig. 23); and distal tip of baculum is partially ossified rather than a solid ossified point.

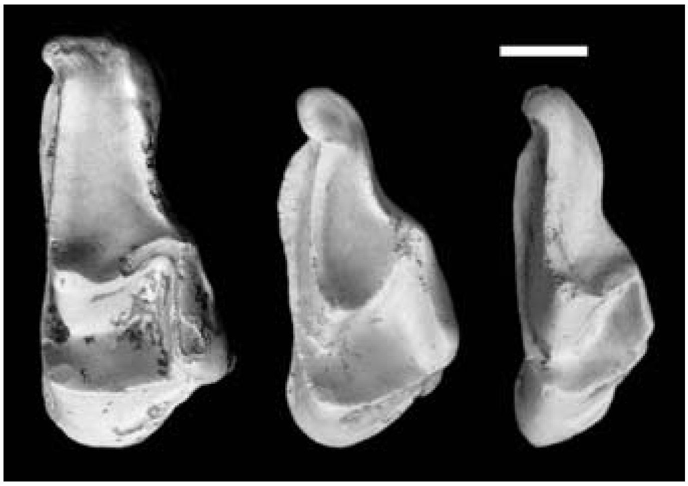


Figure 21. Scanning electron micrographs of M^3 of left, *N. shirleyae* **sp. nov.** (holotype female); centre, *N. bifax* (AM M17299, male); and right, *N. daedalus* (AM M9411, male). Scale bar represents 0.4 mm.

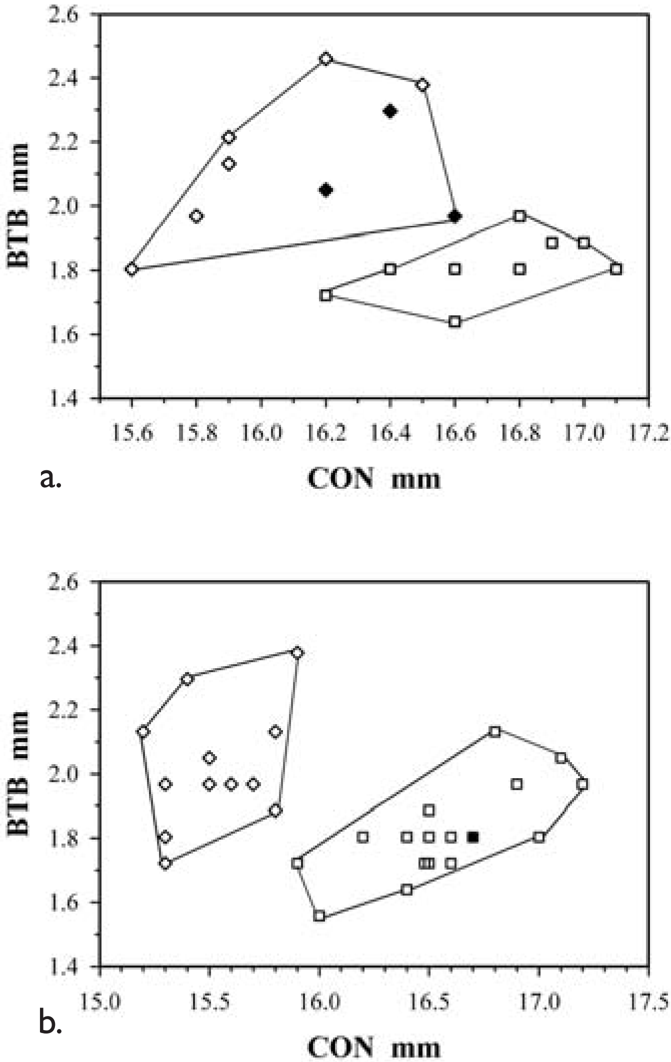


Figure 20. Plots of BTB vs CON for *N. daedalus* (◊) and *N. m. tor* **subsp. nov.** (□), showing the greater BTB in *N. daedalus* for equivalent CON. **a)**, females, solid symbols are females from northwestern Queensland; **b)**, males, solid symbol is specimen from Mt Bruce.

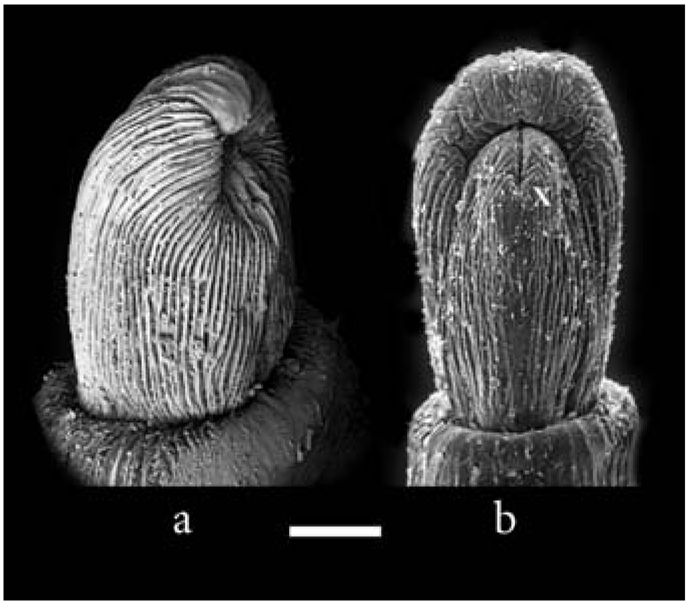


Figure 22. Scanning electron micrographs showing fronto-lateral views of the glans penis of **a)**, *N. bifax* (AM13249); and **b)**, *N. daedalus* (AM M34450), showing the much larger urethral lappets of *N. daedalus* (indicated by X) and the sub-spherical distal knob of *N. bifax*. Scale bar represents 0.5 mm.

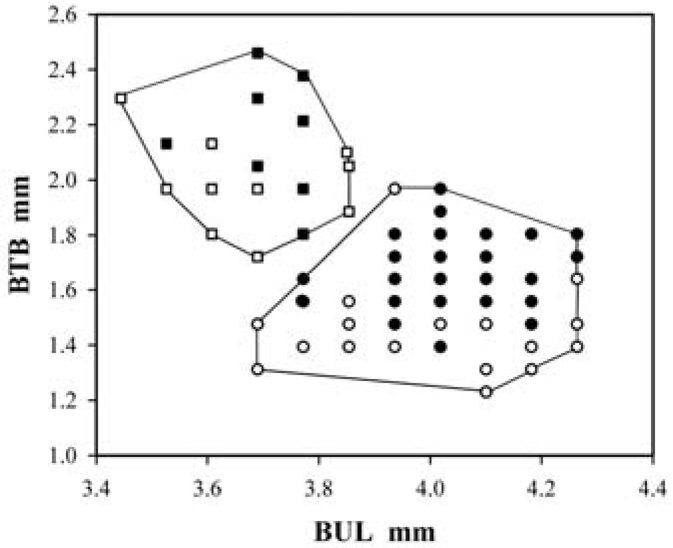


Figure 23. Plot of BTB vs BUL showing separation of *N. daedalus* (□) from *N. gouldi* (○). Solid symbols represent males, open symbols are females.

It differs from *N. nebulosus* in: having paler fur colour; shorter ears for equivalent FA; skull usually relatively broader; narrower INT relative to GL; more reduced protocone on M^1 and M^2 resulting in truncated rather than strongly convex lingual margin; far more reduced third molars, metacone absent from M^3 and third commissure nearly obsolete rather than being well developed and subequal to second commissure; and baculum length > 3.1 mm.

It differs from *N. arnhemensis* in: lighter fur; and other features as outlined for *N. bifax*. *Nyctophilus daedalus* of the same sex are significantly larger than *N. arnhemensis* for most external and cranial dimensions.

It differs from *N. heran* in: having a less developed post-nasal prominence; relatively smaller bullae; and main shaft of baculum thicker distally.

Readily distinguished from *N. howensis* in skull shape and smaller cranial dimensions (e.g. GL < 18.3 mm vs 23.1 mm), and as outlined in the rediagnosis of that species.

Distribution: Extends from the Hamersley Range region of Western Australia across northern Northern Territory to north-western Queensland (Fig. 8). Distributional limits are Weeli Wolli Springs in the west and Lawn Hill in the east. Most records are within 300 km of the coast.

Nyctophilus daedalus is evidently sympatric with *N. major tor* **subsp. nov.** in the Hamersley Range in Western Australia: a single record of *N. major tor* **subsp. nov.** from Mt Bruce is some 70 km west of specimens of *N. daedalus* collected at Cadgeput Springs. In northwestern Queensland, *N. daedalus* is parapatric with *N. bifax*. The most western records of *N. bifax* are from Cloncurry (AM2547 and a specimen reported by Thomas 1915) which is 300 km southeast of Lawn Hill.

Specimens examined: A total of 33, see Appendix. Black and white photographs of the holotype skull and dentary.

Morphological Variation

Considerable variation exists in overall body size, relative ear length, degree of development of the post-nasal swelling, and skull morphology. This variation occurs both within regions and across the range of the taxon; a more detailed evaluation will be presented elsewhere.

A trend of increasing body size from the Pilbara region through to western Queensland is illustrated by a plot of CON vs longitude (Fig. 24) and FA shows a similar pattern. However the variation is not a simple size cline, as demonstrated in a plot of GL vs FA (Fig. 25). The configuration of specimens in Fig. 25 could be interpreted in terms of two sexually dimorphic forms. However, group membership suggested for some specimens in Fig. 25 do not hold when other characters are examined, although there is general agreement with the morphs described below. A reverse trend occurs of decreasing relative ear size (Fig. 26).

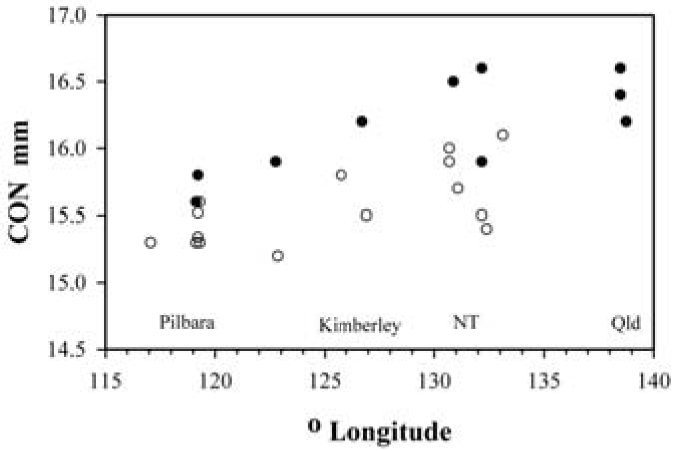


Figure 24. Plot of CON vs longitude for *N. daedalus* showing trend of increasing size of specimens from the Pilbara to western Queensland. Adult females, solid symbols, adult males open symbols.

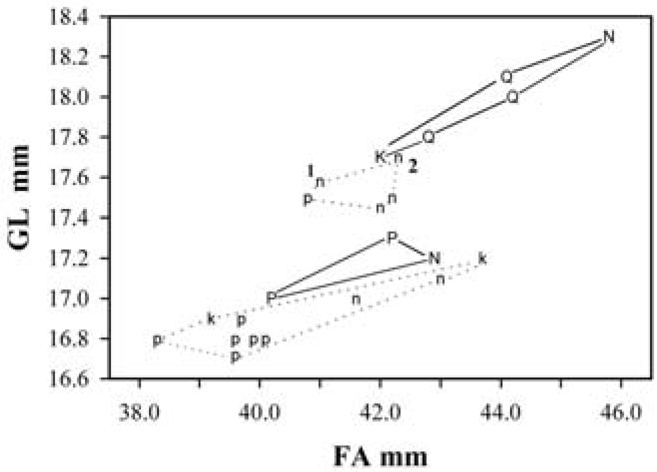


Figure 25. Plot of GL vs FA for *N. daedalus* grouped by sex and putative morph. Localities are P, Pilbara region; K, Kimberley region; N, Northern Territory, and Q, western Queensland. Capital letters represent females, lower case represents male specimens. 1, holotype of *N. daedalus*, 2, *N. daedalus* (AM9411) from the type locality.

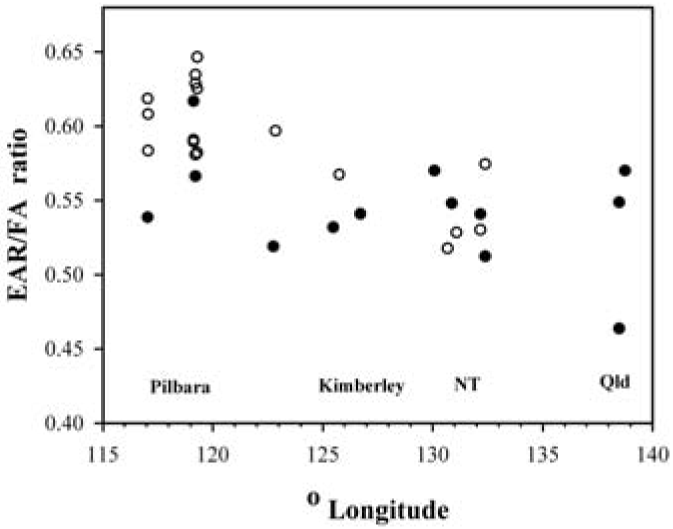


Figure 26. Plot of EAR/FA ratio vs longitude for *N. daedalus* showing trend of decreasing relative ear size between specimens from the Pilbara compared to those of Queensland. Open symbols represent females, solid symbols, males.

Broadly concordant patterns of variation occur between the external characters noted above and the extent of reduction of M^3, relative skull breadth, relative bullar size and distance between bullae. In broad terms, at least two forms are evident within *N. daedalus*, although some individuals are difficult to allocate. These are:

a. larger *bifax*-like animals with relatively short ears, a rudimentary post-nasal swelling, and relatively broader, more robust skulls with reduced third molars and relatively smaller bullae that are clearly set further apart on account of the relatively broader skulls.

b. smaller animals that externally superficially resemble smaller *N. gouldi* in the relatively long ears and more developed post-nasal swelling and less robust skulls. Although most are from the Pilbara, there is a small number of specimens from the Kimberley region and the Northern Territory.

c. a small number of large-bodied animals from the Kimberley region, the Northern Territory and north-western Queensland; these are of equivalent size to larger southern Australian *Nyctophilus*.

The status of several large female specimens from western Queensland (Lawn Hill) requires further clarification and is currently being reviewed. These specimens differ in several skull and dental features from specimens from the Northern Territory and it is unclear whether they represent larger examples of *N. daedalus* or a northern variant of a larger southern taxon such as *N. m. tor* **subsp. nov.** The two specimens from Lawn Hill resemble a pale-furred version of *N. m. tor* **subsp. nov.** in external appearance and fall within the size range of that taxon for several dimensions, e.g. C^1–C^1 (Fig. 27) but they have smaller bullae than *N. m. tor* **subsp. nov.** of equivalent GL. Several large-bodied female specimens from localities in the Kimberley region of Western Australia and the Northern Territory also require investigation but I have not yet examined their

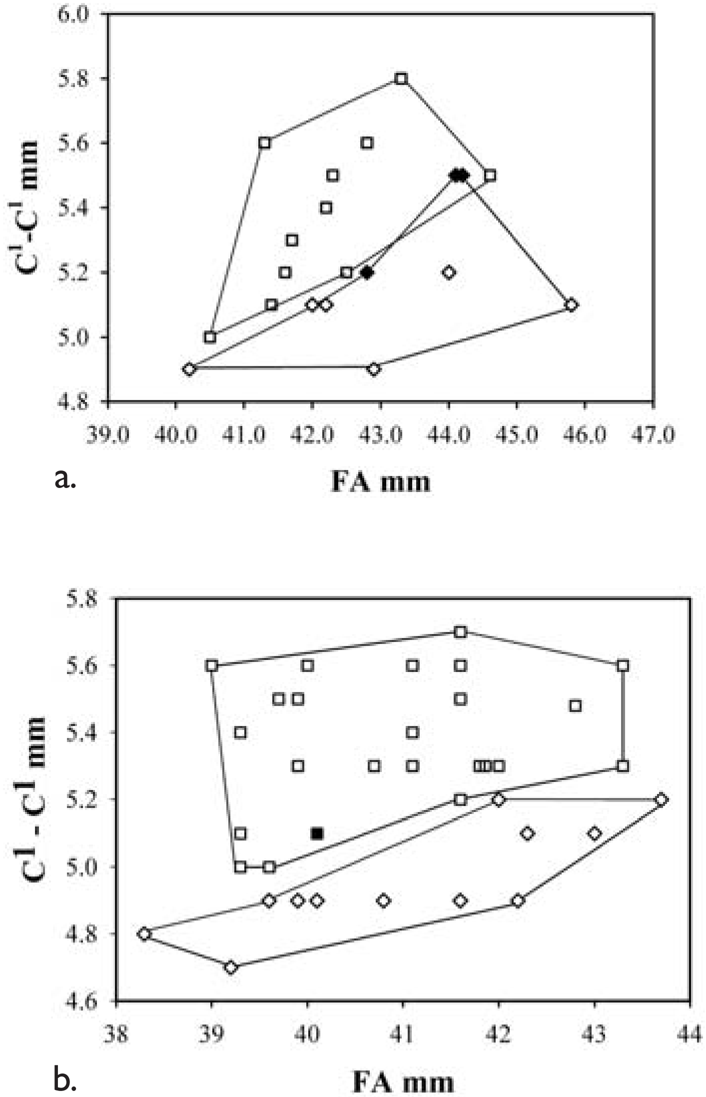


Figure 27. Plot of C^1–C^1 vs FA for *N. daedalus* (◊) and *N. major tor* **subsp. nov.** (□). **(a)**, adult females, solid symbols are three specimens from western Queensland; **(b)**, adult males, solid symbol is subadult from Mt Bruce, Pilbara region.

skulls. Koopman (1984) tentatively assigned an adult female from Port Essington (Northern Territory) to *N. timoriensis timoriensis*, believing it to be distinct from *daedalus* which he regarded to be a subspecies of *N. gouldi*. Measurements of the Port Essington specimen (NHM 47.7.2.1.1) provided by Koopman (*pers. comm.*, 1988) for FA (46 mm), condylobasal length (16.6 mm) and CM^3 (6.5 mm) are comparable to those of the Lawn Hill specimens.

Remarks: There is no doubt that Thomas (1915) was correct in distinguishing *N. daedalus* and *N. bifax* as full species; indeed, as will be suggested below, it is likely that each belongs to a separate major clade within the genus. Pronounced differences exist between the glans penis of these two species: the urethral lappets are much larger in *N. daedalus*, in which there is no trace of the conspicuous spherical distal swelling of *N. bifax* (Fig. 22).

Thomas (1915) listed the simple distal point of the baculum and relative ear length as the main feature differentiating *N. daedalus* from *N. bifax*, which has relatively longer ears and an obvious notch in the distal tip of the baculum. The ten bacula of *N. bifax* examined in the present study all have a prominent distal folk. Thomas stated that the distal tip of the baculum of *N. daedalus* forms a simple point as in *N. gouldi*. In the specimens examined here, the distal tip is only partly ossified and a small cartilaginous groove is visible which is similar to some specimens of *N. major*, although this is likely to be overlooked in dried bacula. Although ear length is relatively shorter than *N. bifax* in most specimens of *N. daedalus* from the Northern Territory, specimens from the Pilbara and the Kimberley region have relatively long ears, similar to *N. bifax* and *N. gouldi*.

When specimens are pooled from throughout their geographic range, mensural ranges for all external and cranial dimensions overlap for each sex between *N. daedalus* and *N. bifax* (Tables 4 and 8). Skulls of *N. daedalus* from the Northern Territory and north-western Queensland differ consistently from *N. bifax* in the more reduced M^3 and in being generally more robust. Thus the zygoma and braincase are relatively wider with a prominent lambdoidal crest. The M^3 of *N. daedalus*, as well as being smaller relative to M^2, has the metacone and premetacristae reduced to a small ridge, and in this respect, is similar to that of *N. m. tor* **subsp. nov.** (Figs 7 and 21).

A specimen of *N. major tor* from Mt Bruce indicates close parapatry between this taxon and *N. daedalus* in the Hamersely Range. The closest records of *N. daedalus* are from Cadjeput Springs and Weeli Wolli Springs, both some 70 km to the east. The Mt Bruce specimen closely resembles an adult male *N. daedalus* from Weeli Wooli Springs (WAM18976) in skull shape but differs in its larger size and in having very shallow compared to deep basioccipital pits. Though not fully mature, this specimen is significantly larger in skull dimensions than four skulls of *N. daedalus* of both sexes from adjoining localities (e.g. GL 18.2 mm vs 16.9 - 17.4 mm) and is well within the overall range of male *N. major tor* **subsp. nov.** (17.2 - 18.75 mm, n = 31). These differences are also evident in a bivariate plot

Table 8. Summary statistics for 11 external and 15 skull and dental dimensions of adult specimens examined of Australian *N. bifax*.

N. bifax

	Female						Male					
	Mean	s.d.	Min	Max	N	CV	Mean	s.d.	Min	Max	N	CV
EAR	24.34	1.385	20.8	27.1	55	5.7	23.62	1.544	19.2	26.7	51	6.5
D1	6.58	0.520	5.1	7.8	50	7.9	6.31	0.615	4.4	8.1	48	9.7
FA	42.74	1.282	39.5	46.8	61	3.0	40.93	1.252	37.5	42.8	61	3.1
D31	39.62	1.110	36.4	42.3	54	2.8	38.64	1.212	36.1	40.8	57	3.1
D32	16.01	0.922	11.1	17.3	48	5.8	15.59	0.618	13.6	16.9	49	4.0
D33	14.96	0.725	13.3	16.6	48	4.8	14.74	0.691	13.3	16.3	49	4.7
D51	39.47	1.111	36.4	41.7	51	2.8	38.33	1.151	36.0	40.7	51	3.0
D52	11.03	0.458	9.9	12.3	49	4.2	10.66	0.432	9.6	11.6	48	4.1
D53	10.16	0.829	8.0	11.5	49	8.2	9.78	1.014	7.3	11.5	49	10.4
HL	21.12	0.934	18.9	22.7	50	4.4	20.57	0.943	18.9	22.3	49	4.6
WT	9.24	1.011	7.7	12.0	38	10.9	8.08	1.122	5.0	11.8	37	13.9
CON	15.71	0.402	14.80	16.50	25	2.6	15.30	0.360	14.60	16.20	43	2.3
GL	17.07	0.410	16.30	17.70	25	2.4	16.78	0.374	16.10	17.70	43	2.2
CM^3	6.43	0.184	6.10	6.80	25	2.9	6.25	0.147	6.00	6.60	43	2.4
C^1-C^1	4.92	0.191	4.50	5.30	25	3.9	4.80	0.174	4.4	5.20	43	3.6
ZYG	10.76	0.257	10.30	11.37	25	2.4	10.59	0.223	10.20	11.00	43	2.1
INT	3.63	0.159	3.30	4.00	25	4.4	3.58	0.154	3.20	4.00	43	4.3
M^3–M^3	7.05	0.236	6.50	7.45	25	3.3	6.87	0.172	6.50	7.20	43	2.5
BRH	6.39	0.184	6.00	6.70	25	2.9	6.34	0.224	6.00	6.80	43	3.5
MAS	9.05	0.235	8.50	9.40	25	2.6	8.88	0.216	8.40	9.50	43	2.4
BTB	2.20	0.110	1.97	2.46	23	5.0	2.16	0.118	1.89	2.46	38	5.5
BUL	3.59	0.095	3.36	3.77	23	2.6	3.52	0.128	3.28	3.85	38	3.6
BAS	5.82	0.227	5.33	6.15	24	3.9	5.66	0.189	5.33	6.15	38	3.3
M^3L	0.89	0.062	0.83	0.97	6	7.0	0.83	0.022	0.80	0.85	5	2.6
M^3B	1.95	0.097	1.78	2.05	6	5.0	1.93	0.096	1.82	2.05	5	5.0
PAL	6.55	0.174	6.33	6.86	11	2.7	6.24	0.287	5.70	6.66	9	4.6

of C^1–C^1 vs FA (Fig. 27). The considerably worn teeth of some of these specimens of *N. daedalus* suggests that their smaller size is not due to age differences. In its larger size, darker fur colour and shallow basisphenoid pits the specimen from Mt Bruce contrasts with *N. daedalus* from adjoining localities yet resembles *N. major tor* **subsp. nov**.

The recognition of *N. daedalus* and *N. bifax* as distinct species raises the issue of the status of *N. arnhemensis*. This taxon closely resembles *N. bifax* in external, cranial, penile and bacular morphology but is smaller overall. However, morphological evidence to be presented elsewhere suggests that *N. arnhemensis* is distinct from *N. bifax*, and also supports the view of Koopman (1984) that *N. arnhemensis* and *N. microtis* from New Guinea are separate species. *Nyctophilus arnhemensis* differs from *N. daedalus* in having darker fur colour, often relatively longer ears, overall smaller size for equivalent sex, and smaller skull size (GL < 16.5 mm). The glans penis and baculum of *N. arnhemensis* resemble those of *N. bifax* in the pronounced distal spherical protruberance, small urethral lappets and conspicuous distal notch in the baculum.

The presence of a large *Nyctophilus* species in northern Australia, comparable in body size to *N. timoriensis* from southern Australia, has been overlooked, apart from Koopman's tentative identification of a Northern Territory specimen as *N. timoriensis* (Koopman 1984).

A clearer diagnosis of *N. daedalus* will rest on clarification of the status and relationships of smaller individuals, particularly those from the Pilbara region.

Nyctophilus sherrini Thomas, 1915

Holotype: NHM no. 52.1.15.50, adult male in alcohol, collected by Ronald Gunn (Thomas 1915).

Type locality: "Tasmania" (Thomas 1915).

Re-diagnosis: Distinguished from all other members of the genus by the combination of: large size (compare tables 4, 8-10); unreduced third molars (see Figs 7, 21 and 29);

Table 9. Summary statistics for 11 external and 15 skull and dental dimensions of adult specimens examined of *N. sherrini.* WT are field weights taken from Taylor *et al.* (1987).

	Female						Male							
	Mean	s.d.	Min	Max	N	CV	Mean	s.d.	Min	Max	N	CV	CG1985-33 male	*N. sherrini* NHM 52.1.15.50 holotype male
EAR	29.00			29.0	1		28.45	1.392	27.2	29.8	4	4.9		
D1	6.70			6.7	1		7.20	0.392	6.7	7.6	4	5.4		
FA	45.20			45.2	1		45.54	0.940	44.30	46.4	5	2.1	46.3	45
D31	42.80			42.8	1		43.36	1.450	41.3	44.9	5	3.3		
D32	16.00			16.0	1		16.28	0.705	15.5	17.0	5	4.3		
D33	13.90			13.9	1		14.14	0.513	13.3	14.7	5	3.6		
D51	41.40			41.4	1		41.54	1.201	40.1	43.2	5	2.9		
D52	11.40			11.4	1		11.36	0.555	10.9	12.1	5	4.9		
D53	9.90			9.9	1		9.86	1.178	8.6	11.0	5	11.9		
HL	20.00			20.0	1		20.64	0.462	20.1	21.1	5	2.2		
WT	13.1	1.5	9.8	14.9	10		12.7	2.3	9.9	18.9	13			
CON	17.28	0.263	16.90	17.50	4	1.5	17.12	0.148	16.90	17.30	5	0.9	-	17.2
GL	18.85	0.404	18.30	19.20	4	2.1	18.85	0.152	18.60	19.00	6	0.8	19.0	18.5
CM^3	6.98	0.126	6.80	7.10	4	1.8	6.84	0.184	6.45	7.00	7	2.7	6.95	6.9
C^1-C^1	5.35	0.129	5.20	5.50	4	2.4	5.31	0.184	4.95	5.50	7	3.5	5.48	4.7
ZYG	11.13	0.299	10.70	11.40	4	2.7	11.10	0.237	10.70	11.40	6	2.1	11.4	11.4
INT	4.13	0.050	4.10	4.20	4	1.2	4.12	0.117	3.90	4.20	6	2.8	4.2	4.0
M^3–M^3	7.55	0.252	7.20	7.80	4	3.3	7.51	0.143	7.30	7.70	6	1.9	7.55	7.1
BRH	6.68	0.126	6.50	6.80	4	1.9	6.68	0.164	6.40	6.80	5	2.5	-	6.35
MAS	9.83	0.171	9.60	10.00	4	1.7	9.82	0.148	9.60	10.00	5	1.5		8.9
BTB	1.83	0.047	1.80	1.89	3	2.6	1.85	0.195	1.56	1.97	4	10.6		
BUL	4.16	0.041	4.10	4.18	4	1.0	4.12	0.037	4.10	4.18	5	0.9		4.2
BAS	6.15	0.116	6.07	6.31	4	1.9	6.00	0.107	5.90	6.15	5	1.8		
M^3L	0.95	0.021	0.94	0.98	4	2.2	0.96	0.024	0.94	0.98	3	2.5		0.84
M^3B	2.14	0.021	2.13	2.17	4	1.0	2.14	0.052	2.09	2.21	4	2.4		2.2
PAL	7.42	0.284	7.20	7.80	4	3.8	7.32	0.117	7.10	7.40	6	1.6	-	7.1

a relatively narrow skull with unexpanded zygoma and narrow rostrum, yet with relatively broad temporal region (see Figs 2 and 28); inflated braincase; and comparatively large bullae (Fig. 28).

It differs from *N. major major* and *N. m. tor* **subsp. nov.** in: relatively larger third molars; a proportionately narrower skull, i.e. relatively less expanded zygomatic arches and relatively broader intertemporal region; and greater lateral inflated of the anterior of the braincase. The baculum shaft is stouter and proximal arms are relatively shorter. It differs further from *N. m. major* and *N. corbeni* **sp. nov.** in a relatively much narrower rostrum and far less robust skull.

It differs from *N. gouldi* in: larger skull size for equivalent sex; slightly broader skull with braincase relatively more expanded; and longer baculum (> 4.0 mm). It is similar in external appearance and size to larger examples of southeastern Australian *N. gouldi*. The skull differs from that species in: a relatively more inflated braincase; slightly less expanded zygomatic arches; generally wider interpterygoid fossa; and relatively greater INT. The baculum resembles that of *N. gouldi* but is larger (baculum length > 4.0 mm, n= 3).

It differs from *N. nebulosus* in: larger in most skull and dental measurements except BTB, e.g. GL > 18.0 mm; relatively narrower skull; relatively larger bullae that are set closer together; and longer baculum, > 4.0 mm (Table 3).

Table 10. Summary statistics for 13 external and 19 skull and dental dimensions of adult specimens of *N. shirleyae* **sp. nov.**

	Mean	s.d.	Min	Max	N	CV	AM37711 8005 f holotype	AM37710 8004 f	AM37712 8025 f	NHM 80.498 f**
EAR	25.33	0.058	25.3	25.4	3	0.2	25.3*	25.4*	25.3*	23.9
D1	8.13	0.153	8.0	8.3	3	1.9	8.3	8.0	8.1	
FA	46.77	1.252	45.5	48.5	4	2.7	46.6*	45.5*	46.5*	48.5
D31	43.63	0.586	43.2	44.3	3	1.3	43.4	43.2	44.3	-
D32	17.70	0.458	17.3	18.2	3	2.6	17.6	17.3	18.2	-
D33	16.93	0.493	16.6	17.5	3	2.9	16.6	17.5	16.7	-
D51	43.87	0.850	42.9	44.5	3	1.9	44.2	42.9	44.5	-
D52	12.60	0.624	12.1	13.3	3	5.0	12.1	13.3	12.4	-
D53	11.13	0.513	10.7	11.7	3	4.6	10.7	11.0	11.7	-
HL	22.97	0.451	22.6	23.5	3	2.1	22.6*	22.8*	23.5*	-
HB	57.67	6.028	52	64	3	10.5	57*	52*	64*	-
TL	49.67	2.08	48	52	3	4.2	49*	48*	52*	-
WT	12.33	0.764	11.5	13.0	3	6.2	12.5*	11.5*	13.0*	-
CON	17.15	0.172	16.9	17.3	4	1.0	16.9	17.2	17.3	17.2
GL	19.03	0.126	18.9	19.2	4	0.7	19.0	19.0	18.9	19.2
CM^3	7.06	0.136	6.9	7.2	4	1.9	7.0	7.1	6.95	7.2
C^1-C^1	5.64	0.079	5.5	5.7	4	1.4	5.7	5.5	5.6	5.7
ZYG	11.58	0.153	11.4	11.7	4	1.3	11.4	11.7	11.5	11.7
INT	3.92	0.147	3.8	4.1	4	3.7	3.8	4.0	4.1	3.8
M^3–M^3	7.64	0.249	7.4	7.9	4	3.3	7.5	7.4	7.8	7.9
BRH	7.13	0.153	7.0	7.3	3	2.1	7.0	7.1	7.3	-
MAS	9.76	0.304	9.4	10.1	4	3.1	10.1	9.65	9.9	9.4
BTB	2.62	0.153	2.45	2.75	3	5.8	2.65	2.45	2.75	-
BUL	3.79	0.131	3.6	3.9	4	3.5	3.6	3.8	3.85	3.9
BAS	6.23	0.208	6.0	6.4	3	3.3	6.0	6.4	6.3	-
M^3L	0.87	0.029	0.85	0.9	3	3.3	0.9	0.85	0.85	-
M^3B	2.08	0.029	2.05	2.1	3	1.4	2.05	2.1	2.1	-
PAL	6.55	0.129	6.4	6.7	4	2.0	6.6	6.7	6.4	6.5
MESO	2.08	0.065	2.0	2.15	4	3.1	2.05	2.0	2.15	2.1
JWL	12.84	0.387	12.45	13.3	4	3.0	12.45	13.0	12.6	-
CM_3	7.59	0.207	7.34	7.8	4	2.7	7.52	7.72	7.34	7.8
M_1-M_3	5.07	0.094	5.0	5.18	3	1.9	5.0	5.18	5.04	-

* field measurements; ** measurements from Hill and Pratt (1981).

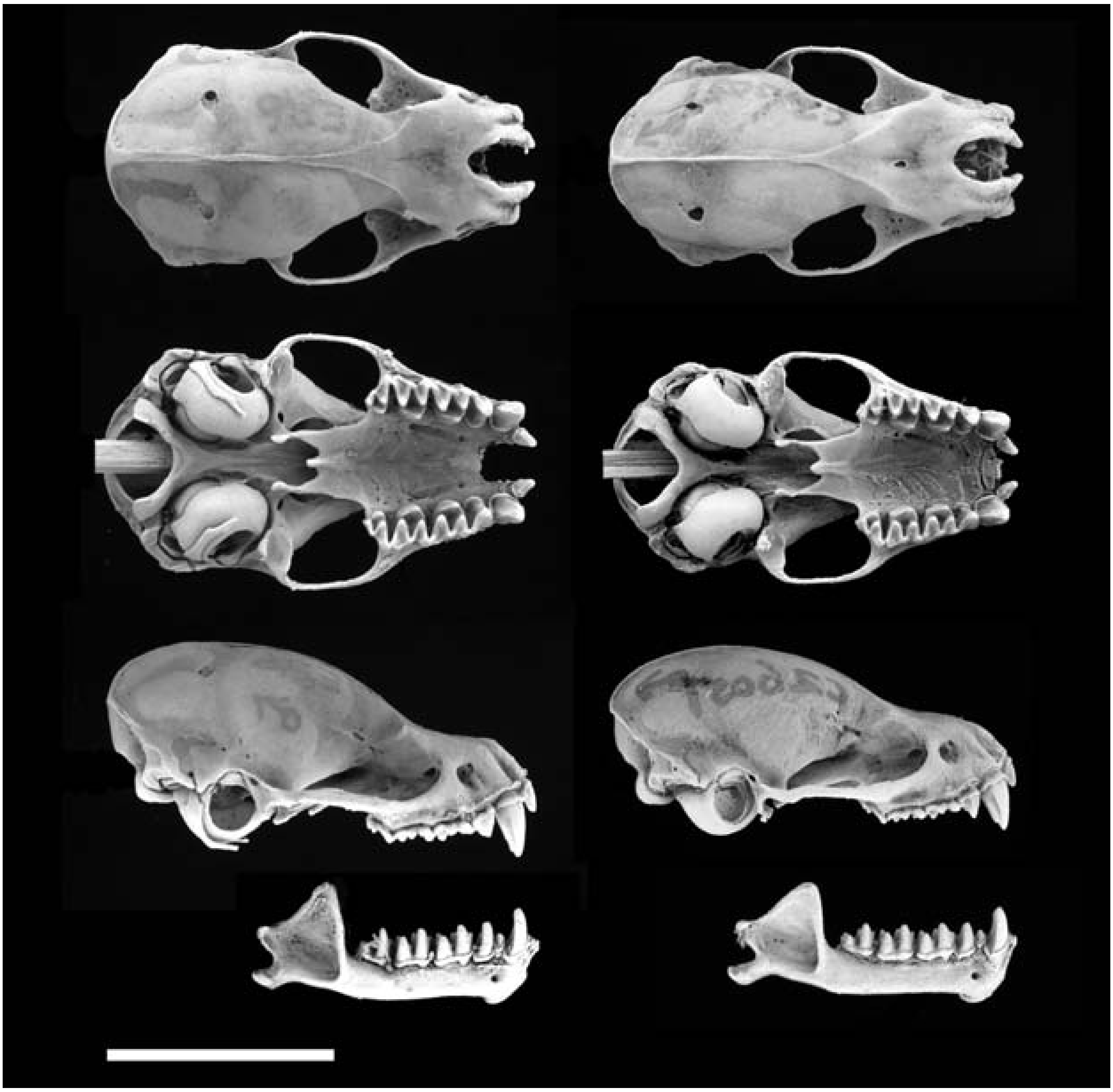


Figure 28. Photographs of the skulls of male, left, *N. sherrini* (AM M34456) from Fortesque Forest, Tasmania; and right, *N. gouldi* (C26051) from Mt Eccles, Victoria, showing the more inflated braincase and broader INT of *N. sherrini*. Scale bar represents 10 mm.

It differs from *N. geoffroyi* in: its larger overall size; reduced postnasal prominence; the distinctive shape of the glans penis; larger baculum; narrower skull; and relatively smaller bullae.

Easily distinguished from *N. howensis*, which has a much more thick-set skull which is larger (GL > 20 mm, CM^3 > 7.5 mm) and flatter, and has a proportionately much larger rostrum.

Distribution: Restricted to Tasmania (Fig. 8) where it is widely distributed, including in the coastal southwest of the State (Schulz and Kristensen 1996), though with relatively few records. Taylor *et al.* (1987) provide a distribution map for this species (as *N. timoriensis*), based on their field work.

Specimens examined: A total of 17, see Appendix. I have examined black and white photographs of the holotype skull and dentaries.

Remarks: In the past most authors have associated *N. sherrini* with Australian mainland populations of *N. timoriensis*, presumably due to its large size. However, of the mainland Australian species, *N. sherrini* most resembles *N. gouldi*, as implied by Hall and Richards (1979) and Richards (1983). Although a relatively small number of specimens of *N. sherrini* were available for this study, it is clear that *N. sherrini* and *N. gouldi* are distinct species. Larger adult examples of *N. gouldi* from Victoria overlap in FA and C^1–C^1 with *N. sherrini* of equivalent sex. Field workers in Tasmania should consider the possibility that *N. gouldi* might also occur in that State. If so, it is not clear at present how these taxa might be distinguished using external criteria, though this might be more evident in live animals than voucher specimens. Ranges of body weights of Victorian *N. gouldi* taken in the field overlap with those of *N. sherrini* given by Taylor *et al.* (1987). Externally *N. sherrini* is also similar to

larger southeastern Australian *N. gouldi*. The overall size of the skull of *N. sherrini* is larger, with a more inflated braincase and the interpterygoid fossa is usually relatively wider. Thus the skull of an adult male *N. sherrini* (AM M34456) from Fortesque Bay, while only slightly larger in most dimensions than a male *N. gouldi* (MV C26051) from Mt Eccles, western Victoria (GL 18.8 vs 18.4 mm; CM^3 6.9 vs 6.8 mm; C^1–C^1 both 5.3 mm; ZYG 11.1 vs 10.5 mm; INT 4.2 vs 4.1 mm; MAS 9.8 vs 9.7 mm; BRH 6.8 vs 6.5 mm) has a much larger braincase which is clearly more expanded anteriorly (Fig. 28). In most cases, the posterior extension of the pterygoids is slightly greater in *N. sherrini*. While the braincase is relatively larger and wider in *N. sherrini*, the zygomatic arches are relatively less expanded, resulting in a generally slightly narrower skull than *N. gouldi*. INT is relatively broader in *N. sherrini*.

Baculum shape is similar in *N. sherrini* and *N. gouldi*, although the proximal end tends to be relatively higher in *N. sherrini* (Figs 5 and 6, Table 3) and the baculum is considerably larger than in *N. gouldi* (length 4.0-4.5 mm, n = 3 vs mean = 3.26, 3.0 - 3.7, n = 26). The glans penis of *N. sherrini* is far narrower than that of *N. gouldi*, being more compressed laterally in the three specimens examined.

Nyctophilus howensis McKean, 1975

Holotype: ANWC CM4724, cranium with periotic bones and dentaries missing, collected by G. F. van Tets. The skull was found on a rock ledge on the cave wall, but post-cranial material was not found with the skull (G. F. van Tets, pers. comm.).

Type locality: Lord Howe Island, "cave at north end of Island, north east of North Bay Beach" (McKean 1975). The skull was found on a mezzanine ledge in Goosebury Cave (Van Tets, quoted in Richards and Hall 1999). A label associated with the type skull notes "cave entrance in vine-covered opening in forest".

Re-diagnosis: Evidently a large bat, as judged by cranial dimensions (see Tables 4, 8-10; Fig. 29). Skull is largest recorded for the genus, compared with maximum measurements of the next largest species, *N. major* and *N. corbeni* **sp. nov.**: GL 23.1 mm vs 20.8; ZYG 13.9 mm vs 13.3; CM^3 8.1 mm vs 7.8; C^1–C^1 6.7 (from alveoli) vs 6.5 (from cingula); PAL 9.4 vs 7.7. Lateral profile of skull is low, unlike any other large member of the genus.

It differs from other large species of the genus, viz, *N. corbeni* **sp. nov.**, *N. major major*, and *N. sherrini* in: ant-orbital foramina being relatively much narrower and smaller; relatively much smaller anterior palatal emargination and narrower rostral sulcus; interdental palate relatively broader and shallower; and interpterygoid fossa width similar in absolute size but relatively much narrower due to larger skull size.

It further differs from *N. m. major*, *N. corbeni* **sp. nov.**, *N. m. tor* **subsp. nov.** and *N. daedalus* in its less reduced M^3, and further differs from *N. corbeni* and *N. daedalus* by a relatively much longer palate.

It further differs from *N. sherrini* by a greater reduction of M^3 and a relatively broader rostrum.

Figure 29. Photographs of the holotype skull of *N. howensis* (ANWC CM4724), sex unknown. Scale bar represents 10 mm.

Distribution: known only from the holotype skull from Lord Howe Island.

Measurements of holotype (mm): GL, 23.09; CON, 21.26; ZYG, 13.88; INT, 4.23; Anterior palatal emargination, diameter, 1.9; Ant-orbital breadth, 6.93; Incisor socket, diameter, 1.27; Canine socket diameter, 1.78; Outer width C^1–C^1 (alv.), 6.71; Inner width C^1–C^1 (alv.), 3.56; CM^3 right side, alv., 8.1; Outer width PM^4-PM^4 alv., 7.59; Inner width PM^4-PM^4 (alv.), 4.48; Outer breadth M^3-M^3 (alv.), 8.71; Inner breadth M^3-M^3 (alv.), 4.34; Glenoid fossa breadth, 2.91; BRH, 7.40; Braincase breadth, 9.76; MAS (incomplete, estimated), 11.3; right side socket for auditory capsule, maximum length, 5.2; maximum width, 4.76; Minimum width of basi-sphenoid between sockets of auditory capsules, 1.5; BAS, 7.55; PAL, 9.46; Mesopterygoid fossa width at root of hamular process, 2.72; Mesopterygoid fossa width at posterior base, 2.51; Foramen magnum breadth, 4.24. McKean

(1975) gives other measurements for dentition. (NB: foramen magnum breadth, braincase breadth, MAS and auditory capsule socket length and breadth were taken in 1991. The right occipital condyle and an adjoining section of the cranial vault, including that forming the border of the auditory capsule socket, is now missing.)

Material examined: the holotype skull.

Remarks: No further material of this species appears to have been reported since its description. This species is clearly not conspecific with any known species of the genus. The general size of the holotype skull is much larger than the largest specimens examined of *N. corbeni* and *N. major* - the largest of the extant species of *Nyctophilus*. Although GL of the holotype of *N. howensis* is only a few mm greater than the largest skull of *N. corbeni* **sp. nov.** (20.8 mm), the skull of the latter is considerably smaller in overall appearance than *N. howensis*. The general form of the skull is more gracile than in *N. corbeni*, and superficially resembles that of *N. sherrini*; no close relationship with the latter taxon is suggested.

The overall morphology of the holotype skull superficially resembles that of large species of *Nyctophilus*. A single large upper incisor socket, and no trace of a socket in the narrow gap between it and the canine alveoli indicates that the specimen has a single upper incisor, as indicated in the original description. Compared to large *Nyctophilus*, the skull of *N. howensis* has a longer palate (Fig. 30a) as noted by McKean, but a comparatively short tooth row (Fig. 30b). The skull is narrow (Fig. 30c) and remarkably flat (Fig. 30d). McKean stated that the palate is much broader than any species of *Nyctophilus*. The rostral sulcus is smaller than in other species of *Nyctophilus* and terminates less posteriorly, as does the anterior palatal emargination, which is also narrower and has an evenly rounded posterior margin.

The morphology of the premolars and molars broadly resembles that of other species of *Nyctophilus*. The shape of M^2 differs from that of *N. major* and *N. corbeni* **sp. nov.** in having both the anterior and posterior sides of the tooth straight. M^3 is reduced, but the second and third commissures are present and subequal, and although nearly worn flat, it is evident that a reduced metacone is present.

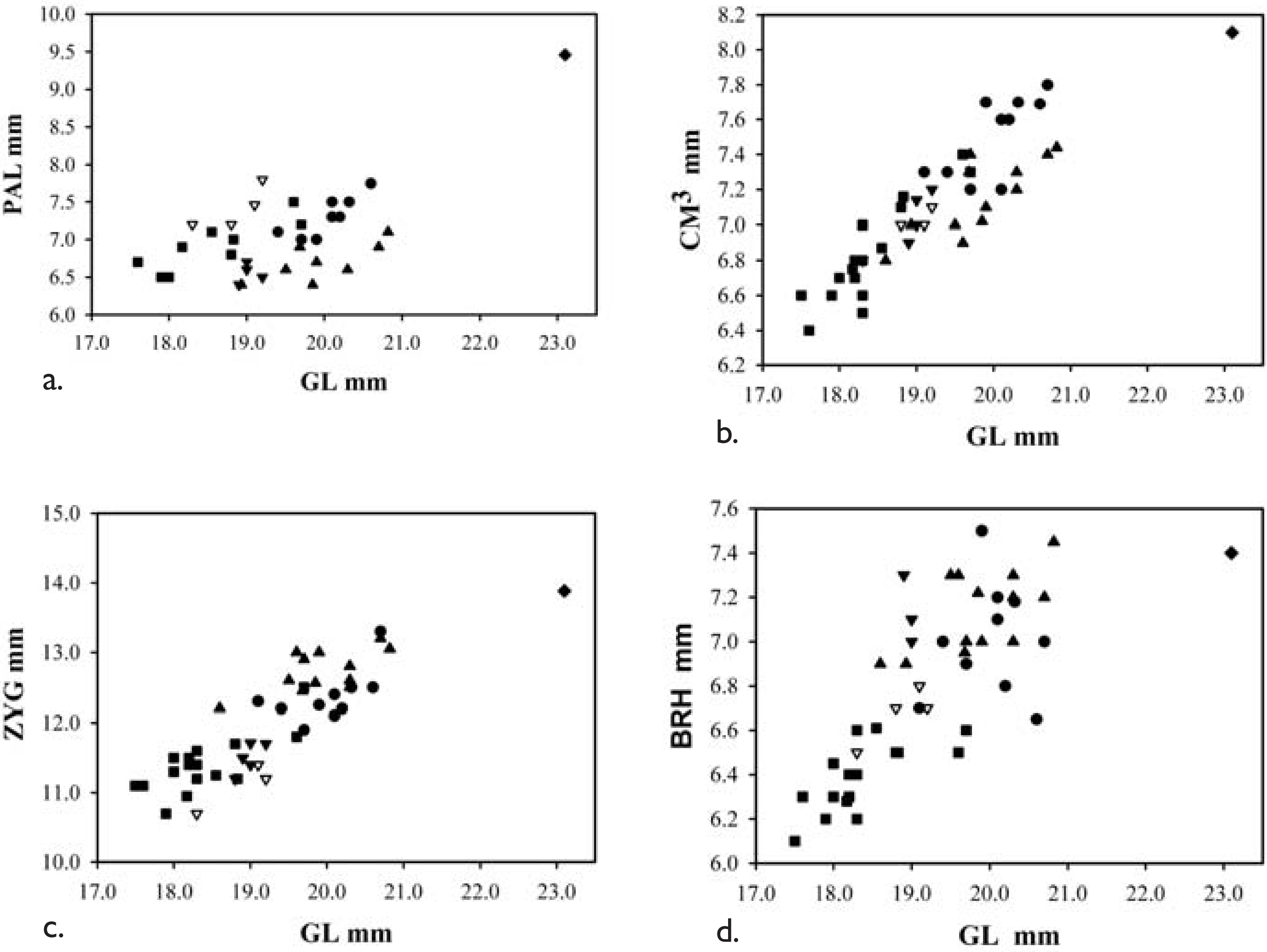


Figure 30. Plots of selected measurements against GL of the holotype skull of *N. howensis* and large species of *Nyctophilus* of either sex, illustrating that *N. howensis* has: **a)**, a long palate; **b)**, a short tooth row; **c)**, a narrow skull; and **d)**, a relatively low braincase. Species symbols are: *N. howensis* (♦), *N. corbeni* **sp. nov.** (▲), *N. major major* (●), *N. m. tor* **subsp. nov.** (■), *N. sherrini* (∇), and *N. shirleyae* **sp. nov.** (▼).

The generic status of *howensis* warrants a more detailed reassessment that is possible here. McKean expressed reservation about placing the taxon in *Nyctophilus,* and I concur. There appears to be no specific reason for assigning the holotype to *Nyctophilus*, other than its superficial resemblance in dental and cranial structure compared to any other genera in the Australian region. The genus *Nyctophilus* is defined by a combination of an abruptly truncated snout with a low horse-shoe shaped narial nose-leaf, a variably developed fleshy postnasal mound, one upper incisor and premolar, ears joined in the midline (except for *N. microtis*) and a relatively slender baculum (Miller 1907; Hill and Harrison 1987). Of these criteria, only the single upper incisor can be confirmed for *N. howensis*. McKean noted the presence of well developed basioccipital depressions which he considered to be characteristic of *Nyctophilus* and the allied genus *Pharotis*. Basioccipital pits occur in a range of vespertilionid genera (DeBaeremaker and Fenton 2003). There appears to be no convincing evidence that the holotype had either a nose-leaf or large ears. McKean interpreted the presence of a rostral depression in the holotype as indicative of a moderately developed nose-leaf which he speculated was possibly of similar development to that of *Nyctophilus timoriensis*. This would have been a reference to the secondary nose-leaf which forms part of a postnasal mound in some species of *Nyctophilus*. However, a wide range of vespertilionid genera contain species that lack any form of nose-leaf or postnasal mound, yet have similar or more developed rostral depressions. Both auditory capsules are missing from the holotype and there appears to be no means of establishing ear size of the holotype. In conclusion, there is little evidence that *howensis* was a long-eared bat on the basis of skull morphology.

Nyctophilus shirleyae sp. nov.

Holotype: Australian Museum number M37711 (field number 8005), adult female, body fixed in 10% formalin and stored in 75% ethanol, skull extracted. Field numbers for tissue samples stored in liquid nitrogen at the Australian Museum are: liver (8005L), kidney (8005K) and heart (8005H). Collected by H. Parnaby in a mist net on Mt Missim, 8 July 1988. Measurements of the holotype are given in Table 10.

Paratypes: Australian Museum number M37710 (field number 8004) adult female, body fixed in 10% formalin and stored in 75% ethanol, skull extracted and in good condition. Captured in a mist net by H. Parnaby on 8 July 1988, at the type locality on Mt Missim. Field numbers for tissue samples stored in liquid nitrogen at the Australian Museum are: liver (8004L), kidney (8004K) and heart (8004H). Australian Museum number M37712 (field number 8025), adult female with regressed teats, body fixed in 10% formalin and stored in 75% ethanol, skull extracted. Captured in a mist net by H. Parnaby on 11 July 1988 on the southwestern slopes of Mt Missim, Kuper Range, PNG: the site (17° 15' S, 146° 47' E) was of higher altitude than the type locality.

Referred specimen: Natural History Museum number 80.498, adult female in alcohol, skull separate, Mt Missim.

Type locality: Southwestern slopes of Mt Missim, Kuper Range, Morobe Province, Papua New Guinea, 17° 16' S, 146° 46' E. The holotype and paratype females were captured in mist nets in mature montane rainforest at an approximate altitude of 1600-1800 m. The exact location and altitude of the type locality and the location of the higher altitude collection site for the paratype M37712 could not be determined but are within about a km radius of the co-ordinates given above. The higher altitude site was close to the main trail leading up the southwestern slopes to the summit of Mt Missim, but the holotype and paratype M37710 were collected on a spur northwest of the main trail.

Diagnosis: Distinguished from all other *Nyctophilus* by the combination of: reduced postnasal prominence (Fig. 31); large skull size (GL for females ≥ 18.9 mm) (Fig. 32 and 33); moderately reduced third molars (Fig. 21); bullae relatively small and set comparatively far apart (BTB > 2.5 mm); and bullae more reduced relative to periotic bone exposing a larger proportion of periotic bone.

It differs from *N. major major*, *N. m. tor* **subsp. nov**. and *N. corbeni* **sp. nov.** in: less reduced third molars in which the metacone is clearly present; smaller bullae (BUL of adult females < 4.0 mm) which are relatively further apart (BTB > 2.5 mm). It further differs from *N. major major* and *N. m. tor* in relatively shorter palate (Fig. 4).

It differs from *N. sherrini* in: relatively broader and more massive rostrum with broader zygomatic archers; relatively smaller INT; posterior extension of the palate relatively shorter; mesopterygoid fossa relatively broader; tympanic bulla relatively much smaller and also absolutely smaller, BUL < 4.0 mm (Tables 9 and 10); and M^3 substantially more reduced (compare Figs 7 and 21).

It differs from *N. daedalus* in: relatively narrower skull; narrower ZYG, C^1–C^1, INT and MAS relative to skull length; a relatively shorter palate (Fig. 4); and considerably less reduced third molars (Fig. 21).

It differs from *N. nebulosus* in: relatively lower post-nasal elevation; in being larger: FA > 45 mm (n = 4) vs < 44 mm (n = 3); larger skull: GL ≥ 18.9 mm; C^1–C^1 > 5.5 mm vs 4.9–5.0 (n = 2); GL much larger relative to FA; a relatively shorter palate; mesopterygoid fossa relatively narrower; INT relatively much narrower; bullae relatively smaller; and in having substantially greater reduction of third molars.

It differs from *N. gouldi* in: relatively lower postnasal prominence; relatively broader skull with a proportionately larger braincase, e.g. BRH for females 7.0 mm and greater, vs mean = 6.19, 5.9–6.6 (n = 42 for the largest populations of female *N. gouldi* which occur in montane New South Wales and Victoria); proportionately much smaller bullae which are set further apart e.g. BTB ≥ 2.45 mm vs mean = 1.71, 1.4–2.0 (n = 37).

Easily distinguished from *N. geoffroyi* which is smaller, e.g. maximum FA for female *N. geoffroyi* from population of largest individuals (Tasmania, n = 13) 41.7 mm vs minimum of 45.6 mm for *N. shirleyae* **sp. nov.**; *N. geoffroyi* has a more developed postnasal elevation with a well developed median membrane joining each prominence that is most developed distally; grey-white tips to ventral

Figure 31. Photographs of the adult female paratype (AM37710) of *N. shirleyae* **sp. nov.** from Mt Missim, Papua New Guinea, taken by H. Parnaby, 8 July, 1988.

fur; relatively much larger bullae, and is smaller than *N. shirleyae* **sp. nov.** in cranial dimensions except BUL: e.g. compared to maximum dimensions of populations of the largest female *N. geoffroyi* (from Tasmania, n = 14): maximum GL 17.1 mm vs minimum of 18.9 mm; CM^3 6.0 mm vs 6.9 mm; $C^1–C^1$ 4.8 mm vs 5.5 mm.

Figure 32. X-ray CT scans of the adult female holotype skull and dentary (AM37711) of *N. shirleyae* **sp. nov.** from Mt Missim, Papua New Guinea. Scale bar represents 10 mm.

Easily distinguished from *N. heran* in: much darker ventral fur; far less developed post-nasal elevation, which is a low rounded mound consisting of a pair of mounds separated medially by a thin vertical groove compared with paired mounds joined medially by a conspicuous membrane that expands distally to form a "Y" shape; being much larger for most dimensions (see Table 10); e.g. FA > 45 mm vs 39.3 mm, GL > 18.9 mm vs 16.7 mm (n = 1), C^1–C^1 > 5.5 mm vs 4.5 mm; and relatively much smaller bullae – BUL = 3.6–3.9 mm v 3.9 mm.

It differs from Australian populations of *N. bifax* in: larger size for most skull dimensions (Tables 8 and 10; Fig. 33), e.g. adult females have GL > 18.0 mm, C^1–C^1 > 5.4 mm; palate shorter relative to GL (PAL/GL < 0.355); GL larger relative to FA (Fig. 34) third molars more reduced: M^3 more reduced than *N. bifax*, second and third commissures shorter relative to first (Fig. 21); and bullae relatively smaller and less developed than *N. bifax* such that a much greater proportion of periotic bone is exposed.

Readily distinguished from *N. microtis* by external features: ears relatively longer and joined at their base by an obvious median membrane, compared with *N. microtis* in which the median membrane is either absent or scarcely visible above the fur; anterior margin of tragus strongly convex rather than straight or weakly convex; larger overall size, e.g. field body weights of adult females > 11 gm vs 9 gm or less (n = 6); dimensions of adult females: FA > 44 mm compared to mean 39.91 mm (38.5–42.7, n = 10), Ear Length > 24 mm, compared to 17.50 (14.9–19.5, n = 7); skull larger: GL > 18.9 mm, compared to mean 15.34 mm (14.5–16.3, n = 8); C^1–C^1 > 5.4 mm compared to 5.0 mm or less (n = 8); CM^3 > 6.9 mm vs mean 5.78 mm (5.4–6.1, n = 8).

Figure 33. Photographs of the dorsal view of the skulls of left, adult female *N. shirleyae* **sp. nov.** (AM37710), showing the larger size and braincase compared to a large female *N. bifax* (CM4508) from Atherton Tableland, Queensland. Scale bar represents 10 mm.

Readily distinguished from *N. walkeri* by much larger overall size, e.g. FA > 37 mm; adult female WT > 10.0 gm; GL > 14.0 mm; C^1–C^1 > 4.5 mm; Ear Length > 16.5 mm and ears relatively much larger; anterior margin of tragus convex as is typical of the genus, rather than straight or weakly concave as in *N. walkeri*.

Easily distinguished in the field from *N. microdon* which has smaller body size: e.g. FA > 45 mm vs < 42 mm, C^1–C^1 > 5.4 mm vs < 4.4 mm; postnasal mound low and rounded compared to two well developed mounds joined in the midline by an obvious elastic membrane; a much smaller tragus relative to ear size; tragus relatively narrower and distal end of tragus rounded rather than truncate; dorsal and ventral body fur grey-brown rather than the rich red-brown of *N. microdon*.

Readily distinguished from *N. howensis* by skull shape and size (the far less inflated cranium of *N. howensis* results in a nearly linear lateral skull profile); a relatively much larger rostrum; skull relatively more elongate; with relatively longer palate and is larger, e.g. GL 23.1 mm compared to < maximum of 19.2; CM^3 is 8.1 mm compared to a maximum of 7.2 mm.

Etymology: I name this long-eared bat after my mother, Shirley Jean Parnaby (nee Slade), a great admirer of the people of the Papua New Guinea nation and its biodiversity, and who encouraged my childhood interest in mammals.

Remarks: This is the largest of the four species of *Nyctophilus* known from New Guinea. It is immediately distinguished in the field from *N. microtis*, which has relatively short ears which lack an obvious membrane that connects the base of the ears; has a narrower tragus, the anterior margin of which is either straight or slightly convex in the midline, rather than being strongly convex; and is conspicuously smaller. It is also easily recognized from each of *N. microdon* and *Pharotis imogene* which are smaller in body size, e.g. FA < 42 mm vs > 45 mm; C^1–C^1 < 4.4 mm vs > 5.4 mm, and both of which have very large ears and large tragi, relative to head size.

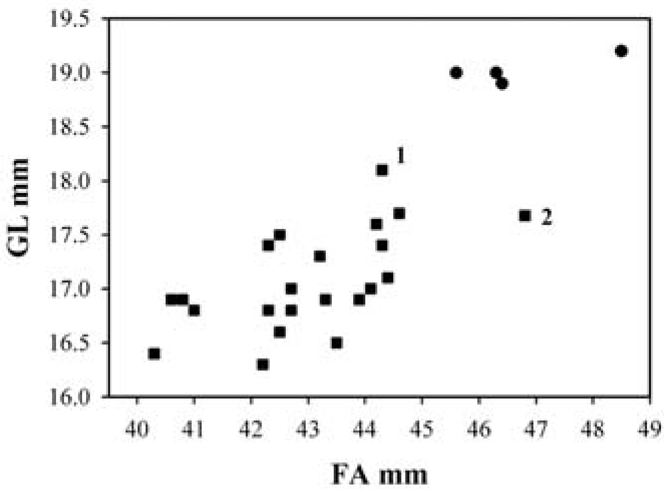


Figure 34. Plot of GL vs FA for adult female specimens of *N. shirleyae* **sp. nov.** (●) and *N. bifax* (■). 1, adult female cf. *N. bifax* (BBM-NG 60073) from Port Moresby, Papua New Guinea; 2, adult female *N. bifax* (CM4508) from Atherton Tableland, Queensland.

In general size and external appearance *N. shirleyae* **sp. nov.** resembles a large version of *N. bifax*. In body size, this species is about the same size as the largest Australian female *N. bifax* that I have examined, but has a relatively much larger skull. Thus although FA lengths overlap, the two species clearly separate on skull size, as illustrated in a plot of GL vs FA (Fig. 34).

Several specimens from New Guinea have been referred to *N. bifax*. Thomas (1922) considered that an adult female (which I have not examined), unfortunately without adequate locality data, compared well with *N. bifax* from Queensland. Tate (1952) regarded a specimen (AMNH 152462) from Idenburg River, northeast West Papua, to be indistinguishable from a series of *N. bifax* from Cape York Peninsula, Australia. Koopman (1982) considered this specimen and another from the Fly River to be quite similar to *N. bifax* from north Queensland, noting that they are at the larger end of the size range. Although the Idenburg River specimen resembles *N. bifax* in skull shape and size (e.g. GL 17.2 mm vs 16.1–17.7 for 43 males) the ears are decidedly smaller than any Australian *N. bifax* that I have examined. The taxonomic status of this specimen is unclear. An adult female (BBM-NG 60073, skin and skull) from Brown River Forestry Station, Central Province, Papua New Guinea resembles *N. bifax* from northern Australia in the relatively long ears and in general skull shape but the skull is larger (GL 18.1 mm vs 16.3–17.7 for 25 adult females). The latter two specimens could well be at least subspecifically distinct from Australian *N. bifax*. Neither appears to represent *N. shirleyae* **sp. nov.**. Other material is assigned to *N. bifax* by Flannery (1995a) and Bonaccorso (1998).

Other than for its large size, *N. shirleyae* would appear to have little in common with the *N. major* complex or *N. sherrini*. It could be most closely related either to the *bifax* or *microtis* species groups, as defined below. The morphology of the glans penis and baculum has not been reported, but these are likely to be highly informative regarding its interspecific relationships. I have not located the adult male reported by Hill and Pratt (1981). Thane Pratt (*pers. comm.* 2005) has suggested that this specimen is likely to be lodged either with the Wau Ecology Institute, PNG, or in the Papua New Guinea National Museum. If the relationships of *N. shirleyae* **sp. nov.** lie with *N. bifax* or *N. microtis*, as suggested by skull and dental morphology, it is likely that penile morphology would consist of a pair of relatively small, narrow urethral lappets and a subspherical distal nob, which is the broad shape for both *N. bifax* and *N. microtis*.

Although currently only known from Mt Missim, it is likely that *N. shirleyae* has a wider distribution within Papua New Guinea, particulary given that bat surveys have not been undertaken in many area. Preliminary examination of specimens recently obtained from the low elevations of the Fly River region, Western Province by Steve Hamilton (pers. comm., University of New South Wales) indicates a close resemblance with *N. shirleyae* and will be reported elsewhere.

Interspecific relationships within *Nyctophilus*

The primary assessment of interspecific relationships within *Nyctophilus* is that of Tate (1941) who recognised four species groups:

a. *timoriensis* group, including *major*, *sherrini* and *gouldi*;

b. *bifax* group with *bifax* and *daedalus*;

c. *geoffroyi* group with *australis*, *pacificus*, *unicolor* and *pallescens* characterized by a highly developed postnasal elevation;

d. *microtis* group, including *microtis*, *bicolor* and *walkeri*.

Tate did not specifically define the characters for each group. He noted the distinctiveness of *N. walkeri* but tentatively placed it within his *microtis* group which he considered to be the most primitive species group. Tate reserved judgement about the taxonomic status of most taxa, many of which were known from few specimens, thus preventing any useful evaluation of within-species variation.

Interspecific relationships of the taxa examined in this study require more detailed examination than is possible here. However, I propose the following tentative arrangement based on an extensive unpublished examination of external features, skull and dentition, and external morphology of the glans penis:

a. A *major* group, consisting of *major*, *m. tor* **subsp. nov.**, *corbeni* **sp. nov**. and possibly *daedalus*. This group has the most extreme reduction of the third molars, and broadly similar external morphology of the glans penis, i.e. comparatively large urethral lappets, the distal portion is simple and lacks any protrusions. The relationships of *N. daedalus* are unclear; it is provisionally included in this group though in some respects it resembles the *gouldi* group. Part of the difficulty could be due to *daedalus* being a composite species.

b. *gouldi* group consisting of three geographic forms of *gouldi*: far south-western Western Australia, inland southeastern Australia and montane and subcoastal eastern Australia; *sherrini* and *nebulosus* are also tentatively included in this group. All have unreduced third molars, and a thick baculum shaft with a solid distal point, (baculum morphology of the south-western Western Australian form of *gouldi* has not been examined in this study) and unadorned glans penis morphology similar to the *major* group. The status of smaller animals from the Pilbara that are currently included with *daedalus* requires further consideration, particularly in relation to eastern Australian inland form of *N. gouldi;*

c. *howensis*, which does not form part of the *major* complex, and differs from all other members of the genus in cranial characters;

d. *microtis* group, with the distinctive *walkeri* tentatively associated. Both have unreduced third molars, small bullae, relatively very short ears and a linear or only

slightly convex anterior tragus margin; and a distinct distal notch in the baculum;

e. *bifax* group, which includes *arnhemensis* – both taxa share small bullae, unreduced third molars and distal baculum bifurcation, and similar penile morphology with the *microtis* group, but have a less specialized postnasal prominence than *microtis* and *walkeri* and the ears are joined medially by a distinct membrane. The relationships of *N. shirleyae* **sp. nov**. remain unresolved but it is provisionally placed with *bifax* which it most closely resembles. The *bifax* group might belong with the *microtis* group.

f. *microdon* – this highly distinctive species differs from all other described species of the genus in the enlarged tragus, distinctive morphology of the glans penis, baculum, and in a number of cranial and dental features. There is no support for the suggestion of Koopman (1984) that *microdon* is closely related to, but more primitive than, *N. geoffroyi*;

g. *geoffroyi* group: previous authors have synonymised *australis*, *pacificus*, *unicolor* and *pallescens* but I have not attempted an evaluation of the status of these forms. Differs in the unique serrated longitudinal dorsal ridge on the distal portion of the glans penis, highly developed snout mound posterior to the noseleaf, and relatively inflated bullae. The affinities of *N. heran* require clarification, athough it is clearly a distinct species from any of the named forms of *geoffroyi*. Kitchener *et al.* (1991) compared *N. heran* with *N. geoffroyi*, and I have tentatively placed it with this group though it differs in penile morphology, which more closely resembles the *gouldi* group and *N. daedalus*.

I have examined external morphology of the glans penis of all currently recognized species except *N. shirleyae* **sp. nov**. and *N. heran* (described and illustrated by Kitchener *et al.* 1991), and *N. microtis bicolor* which is known only from the holotype from Papua New Guinea. My detailed observations on penile morphology will be published separately; however, they suggest the presence of three main groups within *Nyctophilus*:

a. group with large paired urethral lappets, and which lack a pronounced terminal subspherical structure. This includes the *major* and *gouldi* groups defined above and *N. daedalus*, and *N. heran*. It is likely that *N. geoffroyi* also belongs within this clade, though this species complex has a distinctive modification unique in the genus;

b. group in which the paired urethral lappets are relatively much smaller and more elongate than the above clade, and in which a subspherical distal nob is usually present. This includes the *microtis* and *bifax* groups and *N. walkeri* is tentatively placed in this group; and

c. group which has very small, elongate urethral lappets and an entirely different distal structure to either of the above clades. The two species of this group are *N. microdon* and an unnamed species from Papua New Guinea.

A cladistic analysis based on morphological characters is hindered by inadequate knowledge of intraspecific variation, poorly defined species boundaries in some groups (e.g. the *geoffroyi* and *gouldi* groups and *N. daedalus*) and uncertainty over appropriate outgroup comparsions. While it is acknowledged that the species groups recognized here are primarly phenetic and may be based as much on shared primitiveness as on synapomorphy, they are considered a useful step such for a confused and poorly understood genus. A collaborative study with a team led by Belinda Appleton (University of Melbourne) is in progress, in which comparative morphological work will be integrated with a molecular phylogeny of the genus.

Discussion

The central aim of this paper is clarification of the taxa that comprise what has hitherto been referred to as *N. timoriensis*. What has long been regarded as a single widespread species, *N. timoriensis*, is here shown to represent five taxa, at least four of which are full species: *N. major* (including *N. m. tor* **subsp. nov.**), *N. corbeni* **sp. nov.**, *N. sherrini*, and *N. shirleyae* **sp. nov.** In order to clarify the status of *timoriensis*, it was necessary to evaluate variation within a further six taxa, viz. *N. gouldi*, *N. daedalus*, *N. bifax*, *N. arnhemensis*, *N. heran*, and *N. howensis*.

The extent of variation within some taxa is considerable, particularly in *N. daedalus* and *N. gouldi*. A more refined diagnosis of all of these taxa must await a more thorough evaluation of morphological variation, which will be greatly assisted by further collection of material from strategic geographic regions, and the application of molecular analyses. Selection of reliable criteria for field identification is currently hindered by a lack of understanding of within-taxon variation.

Considerable variation within *N. gouldi* was discernable during the course of this study, which will be reported elsewhere. The small size of the inland *N. gouldi* in eastern Australia has been previously recognized (e.g. Parnaby 1987; Lumsden 1994) and small individuals from Queensland were recognized as being different from montane southeastern Australian *N. gouldi* by Churchill *et al.* (1984), who regarded it as a separate unnamed species. Clarification of the status of these forms will greatly facilitate the diagnosis of *N. gouldi* from *N. corbeni* and *N. sherrini*, and the reassessment of *N. daedalus*.

The considerable morphological variation within *N. daedalus* suggests that this is a composite of two, and possibly three distinct forms. Furthermore, if more than one taxon is currently included within *N. daedalus*, they are most likely to be broadly sympatric throughout the current range of *N. daedalus* – a critical issue for field workers trying to identify *Nyctophilus* in northern Australia. A morphological assessment of variation in *N. daedalus* is in progress. Resolution of variation within *N. daedalus* is further necessary to clarify its diagnosis relative to *N. gouldi*, *N. bifax*, *N. m. tor*, *N. nebulosus* and *N. heran*.

Description of the new species and subspecies taxa in this paper represents a step towards resolving the number of species and their diagnosis within *Nyctophilus*. However, the determination of species within this complex genus should be considered a work in progress. A substantial number of issues require resolution before it can be confidently assumed that the majority of taxa have been recognized, let alone adequately diagnosed.

Geographic regions for further strategic collecting

A number of geographic areas can be identified in which further strategic collecting is required to further clarify species limits of the taxa covered in this paper:

1. Additional material is required to define the extent of infra-specific variation within *N. major* from the far south-west of Western Australia, as it is known from relatively few voucher specimens and basic data such as body weights are not available. In particular, further work is needed in areas of potential sympatry between *N. major major* and *N. m. tor*, such as the wheatbelt region of south-western Western Australia (e.g. the Katanning and Narrogin districts), the Roe Plain and Madura districts and surrounding region south of the Nullarbor and the Balladonia district.
2. Given the considerable variation within populations currently referred to *N. daedalus*, it is important to target the entire range of that taxon: the Pilbara, Kimberley, the northern Northern Territory, and northern inland Queensland. Field workers active across that entire region should be alert to any *Nyctophilus* that is not obviously *N. walkeri* or *N. geoffroyi* – I also anticipate difficulties with remaining species including *N. arnhemensis*.
3. A transition zone between the smaller inland form of *N. gouldi* and the larger montane and subcoastal form of *N. gouldi* should be examined to determine the relationships of these morphologically distinct populations; the smaller inland form extends from northern Victoria to northern Queensland.
4. Further survey work is required in Tasmania, where forest environments are currently undergoing accelerating and already severe degradation from clear-cut logging operations. This is necessary, both to obtain more material of *N. sherrini*, which is very poorly represented in world research collections, and to determine whether *N. gouldi* also occurs in Tasmania. If the latter species does occur there, it is likely have been confused with *N. sherrini* in the past, particularly because identification of *Nyctophilus* species would most likely have been based on the presence or absence of a distinctive Y-shaped groove on the post-nasal bump, which is characteristic of *N. geoffroyi*, and general body size.
5. Extensive survey work is needed in Papua New Guinea and West Papua, and more widely in eastern Indonesia, both in rainforest and in eucalypt savannahs. Few specimens exist of *N. shirleyae* and the status of the small number of specimens assigned to *N. bifax* from those regions needs clarification.
6. Efforts should be made to obtain further material of *N. howensis*, including post-cranial material, from cave deposits on Lord Howe Island.

Field workers in all regions should anticipate ongoing difficulties in identifying *Nyctophilus* – reliable field criteria cannot be derived until species diagnoses are refined, which in turn requires further collecting of the many poorly represented taxa to assess intraspecific morphological variation. Unfortunately, recognition of the imperative to retain voucher specimens has declined in Australia over the past decade or so. There has been a significant increase in field work but a decrease in the number of voucher specimens being lodged in museums. This has probably arisen from a combination of factors, one being a failure to appreciate that species taxonomy is unrefined for many taxa. It is generally assumed that taxonomic confusion is confined to a minority of taxa, whereas the reality is that many genera of Australian mammals (and other vertebrates) remain poorly resolved.

Management implications

The results of this study provide yet another reminder of the imperative of a refined understanding of species taxonomy and the implications of species taxonomy for effective conservation management strategies – a recurrent theme in the literature of Australian mammals. For example, one of the most intensively studied Australian mammals, the small dasyurid *Antechinus stuartii*, was shown to consist of four largely allopatric species with restricted distributions (Dickman *et al.* 1998; Van Dyck and Crowther 2000). Many other examples could be cited for Australian mammals and many more can be anticipated in the coming decade.

Despite the implications of unrecognized species for effective conservation management, and consequently the obvious relevance of taxonomic studies, species taxonomy still appears to be perceived as either an irrelevancy, a low priority by managers and funding bodies alike, or as the domain of academic research rather than management, i.e. someone else's problem. Paradoxically, academia itself tends to view taxonomy as applied science, at best, and unworthy of pursuit or reward. In my opinion, reasons for the neglect by managers of something as fundamental as species taxonomy for a high profile group like mammals, should be sought in the ideological, political and social arenas. Consequently, the taxonomic impediment of confused species limits of Australian Microchiroptera discussed, for example, by Wood Jones (1925), Frith (1973), Hamilton-Smith (1974), Parnaby (1991) Richards and Hall (1998) and Reardon (1999), still remain substantially unresolved.

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APPENDIX 1

Registration number	N	Locality	State	Lat.	Long.
Nyctophilus corbeni sp. nov. (n=64)					
AM5282, AM5515	2	"Calumet" 26 ml N of Binnaway	NSW	31 17	149 44
AM36753–55	3	Arakoola Nature Reserve	NSW	29 18	150 48
AM36635	1	Arthurs Seat State Forest	NSW	29 21	150 59
AM33176	1	Attunga State Forest	NSW	30 56	150 54
AM36636	1	Baldwin Range, Manilla	NSW	30 38	150 35
AM36883, 36734	2	Bebo State Forest	NSW	28 50	150 55
ANWC31	1	Buddigower Nature Reserve	NSW	34 05	147 05
ANWC24479	1	Bullock Creek, W of Echucha	Vic	36 13	144 12
AM11160	1	Cocopara NP	NSW	34 15	146 15
AM7946	1	Copeton	NSW	29 55	151 01
SAM11329-30, SAM11765-11771, AM35880, AM37585	11	Dangali Nature Reserve	SA	33 12	140 39
C5195	1	Deniliquin, NSW	NSW	35 32	144 57
AM36715	1	Dubbo City centre	NSW	32 14	148 36
AM25355-56	2	Dunsandle Station	NSW	29 08	146 24
AM34675	1	Goonoo State Forest	NSW	32 04	148 54
AM36880	1	Hell Hole Creek	NSW	30 05	150 19
ANWC4910	1	Lake Cowal	NSW	33 42	147 21
C28470	1	Lake Mournpall, via Hattah	Vic	34 43	142 21
AM3909	1	Millmerran	Qld	27 53	151 16
AM37639	1	Moonbi	NSW	31 01	151 04
C3240	1	Mopoke Tank, 30 ml W of Hattah	Vic	34 46	141 46
ANWC4385-86	2	Mt Pluto	Qld	25 00	147 05
AM35881, AM37586	2	Mungo National Park	NSW	33 15	145 00
AM36759	1	Horton River private property	NSW	30 21	150 19
AM37645	1	Pilliga East State Forest - Clay Dam	NSW	30 35	149 26
AM37644	1	Pilliga East SF - Delwood Dam	NSW	30 47	149 42
AM37717, AM37721-22, AM37732-33	5	Pilliga Nature Reserve, Borah Ck	NSW	30 58	149 32
AM38831-35	5	Pilliga East: Gilgai Flora Reserve	NSW	31 00	149 21
AM36878-79	1	Plagyan State Forest	NSW	30 27	150 17
AM36877	1	Plagyan State Forest	NSW	30 27	150 13
SAM10003	1	Sandfords Dam	SA	33 20	140 54
AM36934	1	South Warialda State Forest	NSW	29 43	150 36
SAM9777	1	Tipperary Dam, Morgan Vale	SA	33 14	140 43
AM32038	1	Top Hut Homestead, 8.9 km W	NSW	33 32	142 54
AM36082	1	Warrabah NP -Mt Kapitar	NSW	30 33	151 00
AM36761	1	Woodsreef TSR	NSW	30 21	150 46
SAM490	1	Yarrock	Vic	36 17	141 12
AM23540-23541	2	Yathong Nature Reserve	NSW	32 38	145 33
Nyctophilus major major (n=43)					
WAM18829	1	2 km from Boddington	WA	32 47	116 28
AM37643	1	70 km SE of Perth	WA	32 20	116 15
WAM2955, 2958	2	Albany	WA	35 00	117 52
WAM28057	1	Albany, Kalgan River	WA	34 31	117 43
WAM6715	1	Broadwater	WA	34 29	115 41
WAM1268	1	Chorkerup Siding =?Chorkerrys	WA	34 50	117 41
AMNH197280	1	Contine	WA	32 50	116 50
WAM16850, 16853, 24018	3	Dwellingup	WA	32 38	116 03

APPENDIX I

Registration number	N	Locality	State	Lat.	Long.
Nyctophilus major major continued.					
WAM24862-63	2	Forest Grove	WA	34 04	115 06
WAM6094	1	Mundaring	WA	31 57	116 08
SAM522	1	Greenbushes	WA	33 51	116 03
WAM6375	1	Katanning	WA	33 41	117 33
WAM24547	1	Ludlow	WA	33 37	115 29
MG, unregistered	1	Perth	WA	31 57	115 51
AM4573, AM5473-79, AM5774, AM6319-20	11	Tambellup	WA	34 02	117 38
WAM7666	1	Vasse	WA	33 40	115 15
WAM1247	1	Wonnerup	WA	33 38	115 26
AM M39797-98, M39808	4	Northcliffe	WA	34 47	116 04
AM M39800	1	Dwellingup	WA	32 37	116 01
AM39814	1	Waroona	WA	32 48	116 01
WAM6335-6, WAM6363, 6367	4	Woodanilling	WA	33 34	117 33
WAM22953	1	Kuthala Pass via Mundrabilla	WA	31 49	128 13
WAM28398	1	Nullabor - Madura Quad 2	WA	33 07	127 21
Nyctophilus major tor subsp. nov. (n=92)					
Registration number	N	Locality	State	Lat.	Long.
WAM28400	1	Nullabor	WA	?	?
AM35884	1	Nullabor, Eyre Highway, (car grill)	WA/SA	?	?
WAM17431	1	Jibberding area: White Well	WA	29 50	116 56
AM37933-37934, M39774-75, M39779, M39792, M39804-05.	8	Dryandra woodlands	WA	32 53	116 58
AM37642	1	Woodanilling	WA	33 34	117 33
AMNH197281	1	Katanning	WA	33 41	117 33
WAM14847	1	Kodjkodjin	WA	31 26	117 46
WAM15163	1	Mt Bruce	WA	22 37	118 08
WAM9916	1	Dragon Rocks Reserve	WA	32 49	119 05
WAM17725	1	Marda	WA	30 13	119 16
WAM20697	1	Die Hardy Range	WA	29 57	119 26
WAM20696	1	Mt Manning Range	WA	30 00	119 36
WAM17763-64	2	Bungalbin Hill	WA	30 14	119 49
WAM20166	1	Woodline area	WA	31 50	122 19
WAM23364	1	Queen Victoria Springs	WA	29 53	123 30
AM4976	1	Booanya via Balladomia	WA	32 46	123 36
WAM28399	1	Nullabor - Balladonia Quad 3	WA	32 04	124 03
WAM8735	1	Madura, 12 ml S	WA	32 05	127 04
WAM28402	1	Nullabor -Madura Quad 2	WA	33 07	127 21
WAM28401	1	Nullabor - Madura Quad 4	WA	32 13	127 26
unreg, field nu. 112-012	1	Great Victoria Desert	WA	28 20	127 56
WAM22944, 22949, 22951-52, 22954, 22962, 22967-68, 22973	9	Kuthala Pass via Mundrabilla	WA	31 49	128 13
SAM11296	1	Red Gate Tank, 3km S	SA	31 23	131 16
SAM14285	1	Maralinga, 8.5 km SW	SA	30 13	131 31
SAM14286-87	2	Maralinga, 12 km SSW	SA	30 16	131 33
SAM9325, 9327-9329, 9331-9332, 9334-9342, AM21170-21172	18	Maralinga	SA	30 10	131 35
SAM11288	1	Nanwoora Well, 6 km S	SA	31 25	131 36
SAM14288	1	Maralinga, airstrip	SA	30 09	131 37
SAM14280-14284	5	Ooldea Siding	SA	30 28	131 59
SAM14279	1	Immarna Siding	SA	30 33	132 08
SAM14292	1	Mount Christie Siding	SA	30 55	133 16

APPENDIX 1

Registration number	N	Locality	State	Lat.	Long.
Nyctophilus major tor subsp. nov. continued.					
SAM14289	1	Yumbarra Conservation Park	SA	31 47	133 25
SAM14291	1	Mt Finke, 2 km E	SA	30 55	134 02
SAM14290	1	Mt Finke, 11 km NE	SA	30 52	134 06
SAM13337	1	Calpatanna Water Hole	SA	33 01	134 21
SAM15020	1	Karcultaby	SA	32 46	134 58
SAM12396	1	Gawler Range, Yandinga Wells	SA	32 33	135 19
SAM11363	1	Hambidge Conservation Park	SA	33 26	135 47
SAM10315-10320	6	Lake Gillies	SA	32 58	136 45
AM39782, M39815	2	Jaurdi Station	WA	30 46	120 07
AM38843-38845	3	Goongarrie	WA	29 59	121 03
AM35879	1	Cowell	SA	33 41	136 55
AM39801	1	Eagle Rock, Goldfields district	WA	30 26	118 40
AM38842	1	Balladonia	WA	32 15	123 25
AM39802	1	Balladonia	WA	32 18	123 32
SAM13004	1	Iron Baron	SA	32 58	137 07
Nyctophilus daedalus (n=33)					
WAM15898	1	Beverley Springs Homestead	WA	16 43	125 28
AM34453	1	Blackfellow Creek	NT	13 45	130 52
WAM22356-58	3	Cadgeput Springs	WA	22 46	119 08
WAM22557	1	Cocky Well	WA	16 40	122 45
AM22126-28	3	Corktree Bore, Pilbara region	WA	22 47	119 18
AM9411	1	Daly River	NT	13 45	130 41
AM34450	1	Darwin, 35 k S	NT	12 34	131 05
ANWC7592	1	Deaf Adder Creek Valley	NT	13 06	133 00
SAM6815	1	Doomadge Mission	Qld	17 56	138 45
WAM552	1	Drysdale River	WA	14 07	126 43
WAM14097	1	Drysdale River National Park	WA	15 02	126 55
JM5246	1	Lawn Hill	NT	18 42	138 29
JM5260	1	Louie Ck, Lawn Hill	Qld	18 48	138 30
WAM22558	1	Martins Well	WA	16 34	122 51
WAM19631-33	3	Millstream Station	WA	21 34	117 03
WAM30586-87	2	Millstream Station	WA	21 35	117 04
WAM21578	1	Mitchell Plateau	WA	14 53	125 45
SAM489	1	Palmerston (near Darwin)	NT	12 14	131 18
ANWC4824	1	Rookery Plains	NT	12 32	132 23
AM13351	1	Roper River, Mataranka	NT	14 56	133 07
AMNH216686, WAM18976, unreg. field numbers WA15, WA16	4	Weeli Wolli Spring	WA	22 54	119 13
AM34451-52	2	West Alligator R., junction Highway	NT	12 47	132 10
Nyctophilus sherrini (n=17)					
AM34456-57	2	Fortesque Forest	Tas	43 10	147 50
AM34458	1	Scottsdale, 12 km W	Tas	41 10	147 31
AM37942-43	2	Brittons Swamp	Tas	40 59	144 57
QV1984.1.10	1	Dip Falls	Tas	41 07	145 22
AM34454-55	2	Mole Creek	Tas	41 34	146 24
AM37935	1	Fortesque	Tas	?	?
AM37936-37941	6	Fortesque Bay	Tas	43 09	147 56
CG1985-33	1	Tasmania	Tas	?	?
AM37944	1	Grassy Forest, near Lake Leake	Tas	42 10	147 57